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Created environments voluntarily colonized by Spartina alterniflora in coastal Louisiana

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CREATED ENVIRONMENTS VOLUNTARILY COLONIZED BY *SPARTINA ALTERNIFLORA* IN COASTAL LOUISIANA

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ABSTRACT

The coastal wetlands play a central role in maintaining productivity of the Gulf of Mexico while protecting coastal regions during severe storms. To help offset the loss of coastal marsh, there is growing interest in the beneficial use of dredge spoil for reconstruction of eroded areas. Hydraulic dredges are routinely employed to maintain navigation and the unconsolidated sediments can be pumped considerable distances to create gently sloping wetland areas. Some areas of these reconstructed wetlands are rapidly colonized by *Spartina alterniflora*, the dominant vegetative species in saline areas under tidal influence. Some areas, however, fail to colonize despite favorable positions near the tidal zone. Even where volunteer colonization succeeds, marked differences in vegetative growth are commonly observed. A study was conducted to assess the impact of landscape and edaphic features on volunteer colonization along five transects (40 sites) located in a reconstructed wetland near Port Fourchon LA. Volunteer stands were observed growing 8 cm below to 45.3 cm above mean tide level (MTL). Six of the more productive sites were located at elevations above the mean high water line and the elevation of one of the most productive sites was 30.1 cm above MTL. N deficiency appears to be the primary determinant of overall productivity of *S. alterniflora* in this marsh, and is more acute in areas receiving lower accumulations of organic matter. The organic C and total N contents of sediments in optimal environments were 11 g C kg^{-1} and 0.44 g N kg^{-1}, respectively. Concentrations of >11 g N kg^{-1} in either uppermost leaves or standing biomass were sufficient for optimum productivity. Highly productive plants

also contained higher amounts of P and K and substantially lower amounts of Fe and Al than severely stressed plants. The failure of low-lying areas to colonize appears to be due primarily to an excessive accumulation of salts. These persistently barren areas currently or may have once served as drainage ways with insufficient flow to flush salts to open water, and therefore salts accumulated to a level where colonization is no longer possible

CHAPTER 1 INTRODUCTION

1.1 BACKGROUND

Salt marshes are transitional habitats that exhibit characteristics of both terrestrial and aquatic ecosystems. Generally, these tidally influenced wetlands pose challenging and stressful environments for both plants and animals more accustomed to upland environments or permanently flooded environments.

Wetlands generally include swamps, marshes, and bogs as well as some bottomland forests and similar area. More specially, the U.S. Army Corps of Engineers (COE) has defined wetlands as “those areas that are inundated or saturated by surface or ground water at a frequency and duration sufficient to support, and that under normal circumstances do support, a prevalence of vegetation typically adapted for life in saturated soil condition”. Exact criteria regarding soil characteristics, hydrology, vegetation types and landscape location have been established to precisely delineate wetlands.

While salt marshes occur all along the coasts, over half of North America's coastal wetlands border the Gulf of Mexico (NOAA/USWFS, 1991). The entire coast of Louisiana is occupied by extensive salt marshes, which grade into brackish marshes, then into freshwater marshes in the upper Mississippi River Delta. Salt marshes serve as the interface between sea and land and serve as important economic and environmental resources to Louisiana and other coastal states. Benefits of natural wetland to coastal populations include buffering storm impacts, storing and conveying floodwater, and

absorbing nutrients, sediments and contaminants. Coastal wetlands have high biological productivity and biodiversity and serve as a nursery ground for fish, habitat for wildlife, and a base for many ecosystem food webs (Smith 1993).

Louisiana contains about 40% of the wetlands in the contiguous United States, however, these valuable coastal wetlands are disappearing at an alarming high rate (Figure 1-1). Estimates of coastal land loss range between 65 and 90 km^2 yr^{-1} (Dunbar et al. 1992, Barras et al. 1994). At least 3460 km^2 of coastal marshes converted to open water areas between 1956 and 1990 (Bourne 2000). These losses are primarily the result of a combination of factors including rising sea level, subsidence due to ground-water use and natural compression of underlying sediments. Historically, subsidence has been offset by deposition of fresh alluvial sediments during periodic flooding by the Mississippi River. In recent years, the construction of levees and upstream dams as well as soil conservation practices have reduced sediment loading during periodic flooding of coastal marsh. Coastal marshes have also been severely damaged by extensive canal cutting by the oil industry over the past several decades during exploration and drilling for oil and natural gas. These channels gradually widen through wave action, destabilizing and gradually destroying huge tracts of marsh. Sea level rise, subsidence and the network of industry canals render Louisiana's coastal marsh more susceptible to saltwater intrusion (Norse 1993).

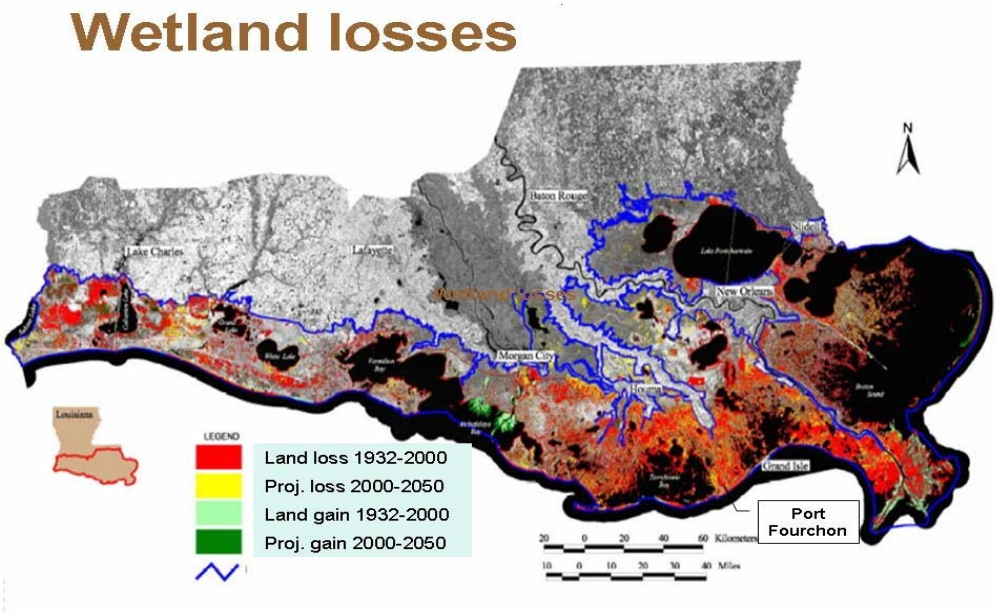

Figure 1-1 Wetland loss in coastal Louisiana (USGS 2003).

Wetland creation offers an opportunity for recreating habitats that support some of the ecological functions that are being lost with the erosion of mature coastal wetlands (Barras 2003). One promising approach currently employed to restore wetlands involves the use of dredge spoil obtained during hydraulic dredging to maintain navigated waterways. Hydraulic dredge spoil may be transported considerable distances and used to recreate eroded wetlands. This spoil, however, often consists of fine-grained, unconsolidated material. Dewatering of these sediments occurs slowly, and recent deposits are highly susceptible to erosion unless vegetatively stabilized to hold the semi-fluid material together and prevent it from washing away during storm events.

Wetland restoration using dredged material is accomplished in several ways. In south Louisiana, dredged material is extensively applied in thin layers to bring subsiding

wetlands up to an intertidal elevation. Dewatered dredged material can be used to construct wind and wave barriers that allow native vegetation to re-establish and restore the viability of a wetland (Ford 1999). These barriers are typically hand-planted to facilitate vegetative stabilization of the dredge material, but success of such plantings is mixed.

Researchers have long recognized that differential tidal inundation of salt-marsh habitats generates severe gradients in soil anoxia (Howes et al. 1981, Mendelssohn et al. 1981) and salinity (Chapman 1974, Jefferies 1977). While it is widely recognized that coastal wetland species will not survive when they are transplanted to marsh elevations lower than their typical range, identifying optimal planting elevations is often difficult in newly constructed areas as the surface rapidly subsides as sediments de-water.

1.2 *S. ALTERNIFLORA*

1.2.1 Distribution

S. alterniflora Loisel, commonly known as smooth cordgrass, saltwater cordgrass, or oyster grass, is a salt-tolerant perennial grass native to the Atlantic and Gulf Coast of North America. It is also found on the Pacific Coast of the United States, where it is considered an invasive species. Spartina species are among the few salt marsh plants that have been introduced outside their native range for erosion control due to their abilities to colonize open areas, stabilize eroding shorelines, and reclaim land.

S. alterniflora is the dominant low salt marsh plant in the intertidal zone along the Gulf Coast, growing from 0.7 m below mean sea level to approximately mean high water

(Landin 1990). One of the primary concerns with the loss of *S. alterniflora* marsh is the corresponding loss of sediments trapped by this species. Sediment accretion rates in *S. alterniflora* marshes along the Gulf Coast can be as high as 13 mm yr^{-1}, with higher stem densities resulting in higher sediment deposition rates and steeper beach profiles (Simenstad and Thom 1995, Gleason et al. 1979). Also, increased sediment accretion may be further changed in water circulation patterns.

S. alterniflora spreads in mid to high tide levels in salt and brackish marshes and is of major ecological importance as a habitat for fish, birds, mammals, and invertebrates, and as primary producer of organic matter for coastal food chains. The stems, roots and seeds of *S. alterniflora* provide food and nesting materials for waterfowl and other wildlife. More than 90% of Louisiana's commercial and recreational seafood species (such as shrimp, flounder and crabs) depend on the protective habitat and nutrients found in coastal wetlands and estuarine waters for much of their lives.

S. alterniflora displays considerable genetic and genotypic diversity, which affects growth and morphology and ecological functions (Proffitt et al. 2003). In the low intertidal zone, *S. alterniflora* is often the dominant species because of its high tolerance of frequently flooding and hypoxia conditions. Very few species can survive the ecological challenge of high salt and too little oxygen. Consequently, even though salt marsh productivity is very high, species diversity is very low. Salt marsh communities are dominated by a few species of halophytes, plants that are adapted for growth and

reproduction in a saline environment. Louisiana coastal marshes are dominated by two species of spartina. In brackish marshes, Spartina *patens* Muhl. is the dominant form. Local names for *S. patens* include cordgrass, wiregrass, marsh hay, and paille a chat tiger (hair of the tiger). In saline marshes, *S. alterniflora* (smooth cordgrass) dominates and as is primarily responsible for productivity of the marsh. *S. alterniflora* communities are sometimes partition into ecotypes, a variant pheonotype of the same species that is adapted to local conditions. Some studies partition *S. alterniflora* into two ecotypes: a tall form that grows in the deeper parts of the marsh, and a short form that grows in more elevated areas (Anderson and Treshow 1980, Gallagher et al. 1988). The height of *S. alterniflora* ranges from 100-200 cm along the creekbanks to <50 cm in the inner marsh (Gallagher et al. 1988). Because nearly monospecfic stands of *S. alterniflora* typically display a gradient in productivity. Smart (1982) partitioned these communities into three relatively distinct height forms along a complex-gradient of environmental factors inward from tidal creek bank. The tall height form (> 100cm) occurs adjacent to tidal creeks and has a high productivity than the more inland short form (< 50 cm), and the medium height from (50-100 cm) is both intermediate in location and productivity.

While recent evidence suggests that the commonly observed tall and short forms may be genetically distinct, numerous studies have demonstrated that the difference in productivity between forms is a function of environmental variables (Mendelssohn 1988, Boyer and Zedler 1999, Seliskar et al. 2002). It is possible that ecotypes like *S.*

alterniflora's tall and short forms occur as a combination of genetic and environmental influences.

1.2.2 *S. alterniflora* Colonization

S. alterniflora plays a pioneering role in the establishment of new marsh. A barren section of sediment is colonized by seed or by rafting of an adult (Collins 2002). Once established, this grass rapidly spreads asexually by means of a subterranean rhizome system. The grass becomes dense and forms a baffle, which encourages the deposition of fine particulate sediment, including organic matter (salt marsh peat). This 'scouring' of sediment from flood waters causes a rise of sediment surface and makes the habitat more terrestrial. Other somewhat less salt-tolerant grasses are then able to invade. Eventually, this series of invasions and takeovers leads to a vertical zonation of grasses and a spread of the entire marsh system (Collins 2002).

Due to vigorous spreading ability and strong underground rhizome growth, *S. alterniflora* has been widely planted to prevent soil erosion and restore wetlands along coastal areas (Matthews and Minellow 1994, Turner and Streever 2002). *S. alterniflora* can also readily colonize barren areas in newly created marsh land. It commonly forms dense stands along the seaward edge of marshes (Metcalfe et al. 1986). In tidal areas with low to moderate wave energy, *S. alterniflora* can colonize a broad range of substrates, ranging from sand and silt to loose cobble, clay, and gravel. It can survive inundation for more than 12 hours a day, pH levels from 4.5 to 8.5, and salinity from 10 to 60 ppt,

though optimal salinities range from 10-20 ppt. (Landin 1990).

S. alterniflora reproduces both sexually and by vegetative fragmentation. During summer, this species develops inflorescences that produce seeds. Seeds appear to require a period of dormancy and have limited longevity (Collins 2002). Once established, *S. alterniflora* spreads vegetatively and forms ring-shaped clumps of individual clones. These clones are tall and conspicuous in open mudflats. New stems grow along the outer edge, gradually increasing ring diameter with each growing season. Vegetative stems die back at the end of each growing season, especially in cooler climates (Ebasco Environmental 1992a). As clones spread they grow into each other and form a dense single-species meadow. The success of *S. alterniflora* can be attributed to its high rate of spread, tall and dense canopy that can shade out other plants, and its ability to colonize low intertidal regions.

While seeds are important for colonizing new areas, they appear to be relatively unimportant in maintaining established stands. Studies in Rhode Island suggest that *S. alterniflora* seedlings are unable to survive under adult canopy, and seedling success increases with the size of bare patches (Metcalfe et al. 1986). Therefore, the expansion of established stands is primarily due to vegetative growth. In some areas, *S. alterniflora* has demonstrated the ability to rapidly colonize bare areas due to a high intrinsic growth rate and rapid propagation of stems via rhizomes (Smart 1982).

Unless newly created marshes are planted, vegetation dynamics seem to follow a

predictable path, with *Salicornia bigelovii* being the first dominant species. *S. alterniflora* expands from the isolated clumps that colonized the new marsh by either rafting in or spreading from adjacent natural marshes. In construction projects along the Atlantic seaboard, *S. alterniflora* replaces *S. bigelovii* as the dominant species after about 5 years and appears to remain so over the long term (Proffitt and Young 1999). A similar pathway of vegetation colonization and succession has been noted for created marshes in southeast Louisiana and other coastal marsh creation projects, though dominance by *S. alterniflora* often occurs more rapidly (Chabreck 1989, Landin et al. 1989).

While the seaward edges of the newly constructed salt marsh are rapidly colonized by *S. alterniflora*, other seemingly similar areas in the intertidal zone remain barren for several years after spoil deposition for unknown reasons. Initially, colonization via seed may be somewhat random, but gradually abundant seed can be seen distributed throughout the intertidal zone. Studies using seed traps (Bruno, 2000) concluded that seed supply in intertidal zones does not limit colonization by *S. alterniflora*. The ability of this grass to colonize some but not all intertidal areas was determined by differences in the microenvironment (Wijte and Callagher 1996, Craft 2001, Lewis 2002).

Even where volunteer colonization occurs, a marked difference in vegetative growth is commonly observed. Dense stands of *S. alterniflora* at lower elevation frequently decline in both height and vigor as the plants develop a few meters inland. These changes appear to be associated with changes in elevation of only a few

centimeters. While differences in the physicochemical properties of the sediments undoubtedly exert an influence on colonization (Wijte and Callagher 1996, Ungar 1998, Lewis 2002), many of these properties are influenced by tidal flood duration (Seneca et al. 1985). The influences of subtle differences in elevation on vegetative growth in coastal marshes are well documented (Lessman et al. 1997, Ford et al. 1999, Proffit et al. 2003).

1.3 ENVIRONMENT SUPPORTING *S. ALTERNIFLORA* COLONIZATION

The development and zonation of vegetation in the salt marsh are influenced by several chemical factors. Plant species of coastal environments are mostly halophytes (Ungar 1991), adapted to cope with saline environments. Soil water salinity and the availability of nutrients, particularly macronutrients such as nitrogen are generally considered two of the most important edaphic factors influencing colonization and productivity. Soil salinity is often linked with landscape features that influence the frequency and duration of tidal flooding. Anderson and Treshow (1980) concluded that the differences in growth response in coastal marshes are both genetic and environmental, with dominant factors being sediment anoxia and salinity stress.

1.3.1 Salinity

In coastal environments, plants are subject to varying levels of substrate salinity and salt spray. Differences in salinity tolerance among and within plant species contributes to the broad zonation of coastal vegetation (Vince and Snow 1984). Plant species of coastal environments are predominately halophytes (Ungar, 1991), adapted to cope with saline environments.

Substrate salinity varies with the time of year and distance from the sea. Salinity is the total content of dissolved inorganic salts in seawater. It is usually expressed as parts per thousand ($^{o}/_{oo}$) which translates to g L^{-1}. The salinity for normal open ocean sea water ranges between $33^{o}/_{oo}$ and $37^{o}/_{oo}$. However, coastal substrate salinity can vary considerably, ranging from $1^{o}/_{oo}$ to $30^{o}/_{oo}$ (Barbour et al. 1985). The more saline waters in coastal marshes are chemically similar to seawater in which the major ions are chloride (55.04 wt%), sodium (30.6 wt%), sulfate (7.68 wt%), magnesium (3.69 wt%), calcium (1.16 wt%) and potassium (1.10 wt%).

Gradients in salinity are ubiquitous features of wetland habitats along the gently sloping northern coast of the Gulf of Mexico. These gradients in combination with depths of tidal flooding have been identified as the major influences on plant zonations in coastal marshes (Mitsch and Gosselink 1993, Odum 1988, Earle and Kershaw 1989). Soil salinity adversely affects a plant species when the accumulation of salts in the root zone exceeds its characteristic tolerance threshold. Most the pore space in wetlands soils is frequently water-saturated, accumulated salts exert a strong osmotic potential that restricts plant roots from extracting soil water, reducing the amount of water plants can uptake (Bauder 2001, Bauder and Brock 2001, Hanson et al.1999).

The dissolved salts in saline waters can also have direct adverse affects on plants. Elevated concentrations of chlorine, sodium, or boron may have a toxic effect on plant roots and may stunt or stop their growth (Saskatchewan 1987, Barbour et al. 1998).

Excessive chlorine accumulation in leaf tissue can lead to cell desiccation, and excessive sodium accumulation can lead to dehydration, reduced turgor, and cell death as sodium displacement of calcium disrupts cell membrane integrity. Elevated sodium can also reduce protein synthesis and alter hormonal activity.

Several studies have concluded that salinity is an important, if not the most important factor in determining the distribution and productivity of *S. alterniflora* (Nestler 1977, Valiela 1982). In many natural marshes, however, the gradient from tall to short plants does not necessarily correspond to a salinity gradient. Valiela (1982), for example, found that plant production in the Great Sippewissett Marsh at Woods Hole, MA was not affected by freshwater irrigation. These studies have demonstrated that plants can recover from temporary salinity stress caused by storm surges and similar episodic events. For example, Howard and Mendelssohn (1999) measured the growth response of four common oligohaline marsh species to short-term salinity increases. Salinity and sulfide concentrations tend to be lower in relatively oxidized creek bank sediments whereas interior marshes tend to be more saline, presumably because these interior areas receive less flushing of salt spray and salts accumulated by evaporation.

1.3.2 Sediment Hypoxia

Wetland soils and sediments are typically waterlogged soils, which are relatively poor in oxygen. Therefore, wetland soils make marshes a very difficult place for most plants to grow and are home to many anaerobic microbes. Upland soils are very porous,

and these pores are usually filled with a mixture of air and water. In waterlogged soils, water displaces air in all pores, reducing both the quantity of oxygen stored in the soil and the rate at which it is replenished by diffusion from the atmosphere. Waterlogged soils rapidly become anaerobic where a suitable organic substrate is available to soil microorganisms. This drastically changes soil chemistry, shifting the balance from an oxidizing to a reducing environment, which may lead to toxic levels of hydrogen sulfide and soluble ferrous iron in the soil. While delivery of oxygen to wetland soils and sediments is possible at the soil-air and soil-water interfaces, diffusion of oxygen through flooded soils is slow.

Many salt marsh plants possess extensive aerenchyma, specialized vascular tissues that can be modified to translocate air to their rhizospheres to create a thin zone of oxygenated soil adjacent to their roots (Jassby and Platt 1976). In the most stressful, highly anaerobic parts of the marsh, plants also rely heavily on anaerobic fermentation in their own metabolism. The rhizosphere is a dynamic environment because the release of oxygen from roots (radial oxygen loss) introduces oxygen into otherwise anoxic wetland sediments and soils and initiates a series of redox reactions that can affect the speciation of elements such as iron, carbon, and sulfur.

Strong redox gradients commonly occur at this interface, and concentrations of many biogeochemically important solutes vary widely, the distribution of electron acceptors (e.g. oxygen, nitrate metal oxides, sulphate, and carbon dioxide) and electron

donors (e.g. dissolved and particulate organic matter, hydrogen, ammonium, methane, ferrous iron, managanous manganese and reduced forms of sulfur) is spatially and temporally heterogeneous. Therefore, redox reactions are closely linked to the hydrology and fluvial geomorphology of the interface. As a result, diverse and variable biogeochemical processes can occur as redox potential, solute concentrations, pH and available sources of energy vary in space and time. Many redox sensitive reactions such as aerobic respiration, fermentation, acetogenesis, methanogenesis, methane oxidation, nitrification, denitrification, metal oxidation cycle important nutrients, (e.g. iron and manganese).

Sulfur and iron oxidation and reduction are of particular interest. Reduced forms of sulfur and iron are potentially toxic to most plants. Transformation between oxidized and reduced states is largely the result of microbial activity in the rhizosphere. Some respiratory microorganisms can use oxidized iron or sulfur as an electron acceptor once oxygen is depleted. When oxygen becomes available, chemoautotrophs rapidly oxidize reduced iron and sulfur. In the rhizosphere of wetland plants where roots supply readily available substrate and oxygen, changes in the speciation of metals and sulfur occur a few millimeters from the roots, affecting their bioavailability and potential toxicity.

Salt marsh plants cope with the potential toxicities that occur under anaerobic conditions in many different ways. For example, although toxic levels of hydrogen sulfide can rapidly form in the reduced sediments of saline marshes, some coastal species

develop plaques of iron oxides on their root surfaces that rapidly react with free sulfides to form insoluble minerals, thereby preventing sulfide poisonings (Mendelssohn et al. 1981). Waterlogged conditions also support the reduction of Fe^{3+} to Fe^{2+} by heterotrophic microorganisms capable of using oxidized iron as an alternative electron acceptor. Reduced iron is much more soluble and excessive uptake by plants can result in acute toxicity. Iron toxicity is more common in freshwater wetlands where low sulfide concentrations can not precipitate a significant portion of reducible iron. In contrast, sulfide toxicity is more common in saline coastal environment where seawater supplies a surplus of sulfate.

1.4 NUTRITION LIMITATION

The nutrients nitrogen (N) and phosphorus (P) are the essential elements that most commonly limit plant productivity in wetland systems. Nitrogen is an integral component of organic compounds such as amino acids, proteins, DNA and RNA. Phosphorus is found in nucleic acids and certain fats (phospholipids). Other elements, silicon and several metals are also often classified as nutrients. Many of the metals present at low concentrations, such as copper, zinc and chromium etc, are essential for life. However, they can become toxic at higher than background concentrations in the environment.

1.4.1 Nitrogen Limitation

Salt marshes are characterized by their large capacity to absorb and store nutrients. Under certain circumstances, these stores are released with subsequent nutrient cycling (Turner, 1993). Mechanisms of nitrogen storage include root uptake, aboveground

assimilation, rhizome storage and sequestration in humic matter (Craft et al. 1988). Considerable seasonal variations in the concentrations of inorganic nitrogen have been observed and these variations are even more marked when exchanges between the different forms of nitrogen (NO_3-N, NO_2-N & NH_4-N) are considered (Langis et al.1991). A corresponding fluctuation in the relative N content of various plant organs as they grow, mature, senesce, and die (Zedler 1993).

In tidal marshes, nitrogen limitation of vegetative productivity has been demonstrated in most studies of N (Jefferies and Perkins 1977, Leendertse 1995, Sullivan and Daiber 1974, Valiela and Teal 1974, Gross 1991). The highly reduced conditions in marsh substrate inhibit nitrification of NH_4^+ to NO_3^-, a form of N that moves readily to plant roots. Therefore $NH_4^+$is the dominant form of nitrogen available to salt marsh vegetation. The low concentrations of NH_4^+ typically found in saline marshes and the relative immobility of this form of N contribute to N limitation (Ungar 1991), but this limitation does not appear to arise entirely from the low amounts of available N present in marsh sediments.

Mendelssohn (1979) found that short plants were deficient in N when compared to tall plants in a *S. alterniflora* marsh in North Carolina. However, the ammonium ion concentration in the interstitial water surrounding the roots of the short plants averaged almost six times higher than that in the tall zone. Apparently, the short plants were not able to fully utilize the available ammonium ions. This inability may be related to more

highly reduced or saline environments. Dissolved sulfide concentration has been positively correlated with interstitial NH_4^+ concentration, suggesting that H_2S toxicity inhibits NH4 uptake and growth of *S. alterniflora*. Reduced N uptake is also related to high levels of salinity (Jefferies 1977, Loveland and Ungar 1983, Drake and Ungar 1989). Salinity may also competitively inhibit NH_4^+ uptake in *S. alterniflora* (Delaune and Pezeshki 1988). The interpretations of factors influencing growth of *S. alterniflora* is further complicated by complex interactions. Broome et al. (1975) measured plant tissue concentration of several nutrients in *S. alterniflora* growing in North Carolina marshes and concluded that that correlations between leaf tissues N: P ratios and aboveground productivity can be used to assess the role of nutrient availability in controlling community structure.

1.4.2 Phosphorus Limitation

The availability of P may also limit N utilization and marsh productivity (Taft and Tyler 1976, Teal 1986, Turner et al. 2004). The concentrations of both nitrogen and phosphorous in salt marsh creeks will depend on the balance between the supply of that component from inside and outside the marsh, the rate of uptake of the component by the growth of salt marsh vegetation, and the factors that influence the availability of these primary nutrients to plants.

Broome et al. (1975) showed that when nitrogen is added, P sometimes became the limiting factor to growth, particularly in coarse textured substrates. Van Wijnen and

Bakker (1999) also found evidence that P limitation occurs in young marshes with low soil organic matter, as well as in both young and old salt marshes when the marsh is saturated with nitrogen. In addition, phosphorus limitation occurs at both successional stages when a marsh is saturated with nitrogen (Stribling and Cornwell, 2001). Even so, a study testing a combination of inorganic N, P and K additions in salt marshes showed N to be the limiting nutrient (Kiehl et al. 1997).

1.4.3 Fertilization

It is now generally accepted that application of N to saline coastal marsh with low N fertility will increase plant productivity. Valiela et al (1978) demonstrated that the addition of nitrogen fertilizer induced short *S. alterniflora* in the inner marsh to grow to heights approaching that of tall *S alterniflora,* while similar treatment had no effect on the growth of the tall form. However, several apparent inconsistencies in that suggest that N fertilization cannot fully restore the potential productivity of *S. alterniflora*. For example, fertilized plants did not achieve the height of tall *S alterniflora* even after 4 yr of treatment. Also, the inner marsh NH_4^+ concentration frequently exceeds that of the creekbank.

1.5 CREATED WETLANDS FUNCTION

Well designed wetland creation and restoration projects attempt to duplicate, as completely as possible, natural wetlands habitats. In the Sabine National Wildlife Refuge (NWR) in southwest Louisiana, created salt marshes formed from pumping hydraulic dredge spoil into formerly open water areas have been compared to nearby natural salt

marshes since 1996. Results showed to the created marshes begin to approximate natural salt marshes as they age, both structurally and functionally (Proffitt et al. 2003, Seliskar et al.2002). Although it takes only a few years for the created marshes to have similar plant species composition as the natural marshes, both being dominated by *S. alterniflora*, older created marshes aren't structurally similar to natural marshes. Soil factors tend to take longer to develop than vegetative components (Craft et al. 1999). Both OM% and bulk density in the created marsh soils are quite different than in the natural marshes; it may take several decades before these factors become equal to values in the natural marshes (Zedler and Callaway 1999).

The similarities in the distribution of plant species in created and natural coastal marshes are clearly related to similarities in elevation. The importance of small changes in elevation in affecting plant species composition is well-known for coastal marshes (Gosselink 1984, Webb and Newling 1985, Landin et al. 1989, Chabreck 1994, Dawe et al. 2000). Differences in salt concentrations and flooding allow for species that are better able to survive and compete indifferent marsh environments to colonize and dominate (Mitsch and Gosselink 2000, Covin and Zedler 1988).

The use of dredge material is a well-known technique for creating or restoring salt marshes that is expected to be common along the Gulf of Mexico coast in the future. However, it is still questionable how effective this method is in producing functioning wetland habitat. If the goal is to produce a marsh dominated by *S. alterniflora*, then that

is easily accomplished (Landin et al. 1989, Streever 2000). Therefore, most wetland scientists advocate the protection of natural wetland habitats to as great of a degree as possible. The massive losses of mature coastal wetlands in recent years, however, suggest that preserving Louisiana's mature coastal wetlands is a daunting task, and efforts to restore lost marsh merit regional and national attention.

1.6 OBJECTIVES

The primary goal of this project is to characterize the environmental factors associated with volunteer colonization by *S. alterniflora* of a restored salt marsh recently reconstructed using hydraulic dredge spoil. A secondary goal is to identify the environmental factors associated with areas that remain barren for more than 12 months after dredge spoil deposition. Specifically, we will seek to establish key relationships between landscape features and sediment physicochemical properties that influence colonization and the productivity of volunteer stands.

Chapter 2 addresses the influence of landscape features such as elevation, duration of tidal flooding, and distance from open as well as ephaphic factors, including salinity, sulfide, and other physiochemical properties of substrates supporting various levels of productivity. Chapter 3 assesses the extent to which N and P limited productivity of volunteer stands and the need for fertilization of marsh constructed from dredge spoil in coastal Louisiana.

CHAPTER 2 RECONSTRUCTED MARSH ENVIRONMENTS VOLUNTARILY COLONIZED BY *S. ALTERNIFLORA*

2.1 INTRODUCTION

Beneficial use of dredge spoil to reconstruct coastal wetlands is a promising technology for offsetting wetland loss in coastal Louisiana (Reed 2002). Hydraulic dredges are typically employed to pump unconsolidated sediments from channel bottoms to create gently sloping wetland areas (Figure 2-1). Rapid establishment of vegetative cover protects these reconstructed wetlands from water and wind erosion and restores ecosystem function (Levin and Talley 2002).

Figure 2-1 During hydraulic dredging to maintain navigation channels (left), a slurry of water and sediments can be pumped considerable distances and discharged at sites where sediments accumulate to form gently sloping marsh land (right).

The shorelines of these created wetlands are often rapidly colonized by *Spartina alterniflora* Loisel, the dominant vegetative species in saline areas under tidal influence in coastal Louisiana. Pioneers appear to originate from water-transported seed and rafting adults, but may also include vegetative propagules deposited during sediment deposition. Once established, these volunteer stands spread rapidly by tillering. Other seemingly

similar areas in the intertidal zone remain barren for several years after spoil deposition for unknown reasons. Initially, colonization via seed may be somewhat random, but after time abundant seed can be seen distributed throughout the intertidal zone. Studies using seed traps (Bruno, 2000) concluded that seed supply in intertidal zones does not limit colonization by *Spartina alterniflora*. The ability of *S. alterniflora* to colonize some but not all intertidal areas appears to be the result of differences in environment (Wijte and Gallagher 1996, Craft 2001, Lewis 2002).

Even where volunteer colonization occurs, a marked difference in vegetative growth is commonly observed. Dense stands of *S. alterniflora* at lower elevations frequently decline in both height and vigor over distances of a few meters. These changes may be associated with changes in elevation of only a few centimeters. While differences in the physicochemical properties of the sediments undoubtedly exert an influence on colonization (Wijte and Gallagher 1996, Ungar 1998, Lewis 2002), many of these properties are influenced by tidal flood duration (Seneca et al. 1985). The effects of subtle differences in elevation on vegetative growth in coastal marshes are well documented (Lessman et al. 1997, Ford et al. 1999, Proffit et al. 2003).

In natural marshes along northern US Gulf Coast, a striking decrease in the productivity and height of *S. alterniflora* with increasing distance from the creek banks is often evident. This productivity gradient has been explained on the basis of several key edaphic factors. While *S. alterniflora* can germinate and seedlings grow in anoxic

conditions and at a salinity of 40 g L^{-1}, the productivity of mature stands appears to be affect by both salinity (Nestler 1977) and reducing conditions that can lead to production of phytotoxic levels of hydrogen sulfide, iron and other elements. King et al (1982) found a sediment sulfide concentration range of 0.09-3.0mM L^{-1} and an inverse correlation between sulfide concentration and biomass of *S. alterniflora*.

The primary goals of the work reported in this chapter were to (1) establish the range in environments within a recently constructed wetland that are capable of supporting volunteer colonization, and (2) to identify edaphic factors associated with differences in productivity within volunteer stands.

2.2 METHODOLOGY

2.2.1 Study Area

This study was conducted near Port Fourchon LA (29° 08' N, 90° 12' W) in a coastal wetland reconstructed using spoil generated by hydraulic dredging of a nearby floatation canal (Figure 2-2). Deposiyion of dredge spoil had been completed about one year prior to initiation of this study in Spring 2004. At that time, volunteer colonizes of *S. alterniflora* dominated the lower lying areas. Glassworts (*Salicornia bigelovii* and *Salicornia virginica*) dominated in upper elevations, though extensive upper areas and lower areas remained barren. Five areas containing stands of volunteer *S. alterniflora* with a range in plant productivity were selected for study.

Figure 2-2 Voluntarily colonized and barren areas of constructed marsh located near Port Fourchon LA. Photo taken in Apr 2004 about 12 months after deposition of hydraulic dredge spoil.

Transects were established in each area originating beyond the shoreline and extending inland until no further colonization by *S. alterniflora* was evident. The first transect (T1) was located in a low-lying area at the end of a narrow, shallow bay lying just inside of the small levee that divided the constructed area from the adjacent flotation canal. This transect originated in open water ~2 m from nearest shoreline vegetation and ranged inland 2 m beyond the point where *S. alterniflora* ceased to grow. The second (T2)(Figure2-3) and third (T3) transects were similar to the first, but were located in somewhat more sharply sloping areas along the same bay as T1. The fourth transect (T4) originated at a small tidal stream that traversed the constructed area and proceeded inland.

The fifth transect (T5) was located in the interior of the reconstructed marsh and originated in a small cut that opened directly into the floatation canal and traversed low-lying areas containing lush stands and broad areas devoid of vegetation despite similar elevations.

Figure2-3 Red flags indicate sample site locations along Transect II at initiation of study (Apr 2004)

On each transect, sampling locations were established to represent a range of biomass productivity. A total of 40 sampling sites were selected along the gently undulating slopes of these transects. Each site was photographed and the location of each site was identified using a Pathfinder Pro XRS GPS (Trimble Navigation Limited, Sunnydale CA USA) to aid in accurate site location during subsequent samplings in the event site marker were lost. Three elevation reference markers were established in low-lying, protected bays connected to the floatation canal by tidal streams by driving 10

cm dia. x 300 cm PVC pipe inserted into the sediment to a depth of ~2 m. The elevations of these markers were referenced to that of a nearby tidal benchmark (NOAA Stn. 8761724A), and the elevation of each site in the study area referenced to the nearest marker. A recording tidal gauge was used to synchronize tidal flow at each study area with a recently established continuously monitoring tidal station (NOAA Stn. 8762075) at Port Fourchon ~2 km from the study areas. These data and marker elevations were used to establish mean tide level (MTL), mean high water (MHW) and mean low water (MLW). The range between MLW and MHW at NOAA Stn. 8762075 averages 32.1 cm and MTL averages 16.2 cm, about 0.2 cm above local mean sea level. These values, in turn, were used to calculate average daily tidal inundation for each site. Datum for Station 8762075 indicates local mean sea level is 32.7 cm above NAVD88.

2.2.2 Plant Sampling

In April 2004, the uppermost fully expanded leaves were collected from 10 plants for elemental analysis. On each sampling occasion beginning in Jul 2004, aerial biomass was harvested in addition to leaf samples by cutting all plants within 0.3 m^2 area at ground level. Plant samples were placed in plastic bags for transport to the laboratory where they were sorted into living (>50 green tissue) and dead *S. alterniflora*. The lengths and diameters of ten randomly selected live plants from each site were measured prior to drying (65^{o}C; 48h) and weight determination. Digital calipers were used to measure stem diameters 4 cm above their base.

2.2.3 Sediment Analyses

Sediment oxidation-reduction potentials were measured *in situ* prior to collecting sediment samples using polished platinum electrodes and a double-junction Ag/AgCl reference electrode. Eh measurements were determined at a 10 cm depth after 15 min equilibration. Electrodes were cleaned and standardized before each use.

Sediment cores (5 cm dia. x 15 cm) were collected in polycarbonate tubes fitted within an AMS Core Sampler (American Falls, ID USA) for analysis of pore water. After collection, the cores were sealed and transported on ice to the laboratory. Bulk surface samples (0-15 cm) of sediment were also collected in each harvested quadrant. Approximate 1 L of sediment from each site was placed in a 4-mil ziplock bag (20 x 25 cm), the air squeezed from bag before sealing, and the sample place on ice for transport to the laboratory for analysis. Field surveys were also conducted to determine the sediments characteristic at all sites. Upon arrival, samples were divided into two portions: one portion was dried (65^{o}C; 48 h) and crushed to pass a 2mm screen for determination of elemental composition; and the second portion refrigerated (4^{o}C) for use in analyses requiring field-moist samples.

Dissolved sulfide concentrations were determined in porewater obtained by packing refrigerated core samples into capped 50 mL polypropylene tubes and centrifuging swinging bucket centrifuge (7000 rpm; 20 min). Tubes were packed full of sediment prior to capping and precautions were taken to exclude as much air as possible.

Sulfide was determined by a method similar to that described by Green and Schnitker (1974). Porewater (25 mL) was extruded into jars containing 25 mL sulfide antioxidant buffer (SAOB) and this mixture titrated using standardized $Pb(NO_3)_2$ and a silver/sulfide electrode to a potentiometric endpoint. The electrode was calibrated prior to each use with a freshly prepared Na_2S solution standardized by the iodometric method (SMWW 4500E).

Electrical conductivity (EC) was determined in saturated paste extracts using field moist samples. Saturated samples were centrifuged and the supernatant collected using a syringe fitted with a 0.45 μm filter. EC was measured in the clear extracts using a calibrated Cole-Palmer Model 410 meter fitted with a 3-pole electrode. Sediment pH was determined in 1:1 soil: water suspensions using a glass combination pH electrode. Dried, crushed soil was used in these analyses and suspensions allowed to stand 30 min prior to pH measurement using a pH meter calibrated at pH 4 and pH 7 using buffer standards. Sediment textural analysis was performed by a hydrometer method (ASTM D422) using field-moist samples after removal of organic matter and salts. Exchangeable cations and cation exchange capacity determined using dried soils using sequential ammonia acetate (pH 7) and KCl extractions (Chapman 1965). Total elemental composition was determined by inductively coupled plasma analysis of HCl: HNO_3 digests.

2.2.4 Statistical Analysis

Table 2-1 Environmental classification of sites along five transects in Jul 2004, Nov 2004 and Mar 2005.

	Jul 2004					Nov 2004					Mar 2005				
Environment	T1	T2	T3	T4	T5	T1	T2	T3	T4	T5	T1	T2	T3	T4	T5
Optimal	0	1	1	1	0	0	1	0	2	0	0	1	0	0	0
Moderate	0	0	3	1	0	1	0	0	1	1	0	0	0	1	0
Severe	2	3	0	4	3	3	4	1	3	2	4	3	2	4	2
Very severe	2	1	1	0	1	0	0	4	0	1	0	0	3	1	2
Barren	1	1	3	4	2	1	1	3	5	2	1	2	3	5	2
Open water	1	1	1	2	0	1	1	1	1	0	1	1	1	1	0

To identify relationships between plant productivity and environmental factors, data were explored using both multivariate and ANOVA analyses. On the basis of these analyses, sites were classified into one of six microenvironments (Figure 2-4). Vegetated sites were classified as ‘optimal’ if they supported between 70% and 100% of the maximum live biomass measured on each sampling occasion. Similarly, sites were classified as ‘moderate’ if they contained between 45% and 70% of the maximum live biomass, ‘severe’ between 15% and 45%, and ‘very severe’ if they contained between 1% and 15% of the maximum live biomass at time of sampling. Non-vegetated sites with elevations greater than the vegetated shoreline were classified as ‘barren’ whereas

non-vegetated sites with elevations less than the nearby shoreline were classified as 'Open water'(figure 2-3). The number of each classification within the five transects at each sampling period are shown in Table 2-1.

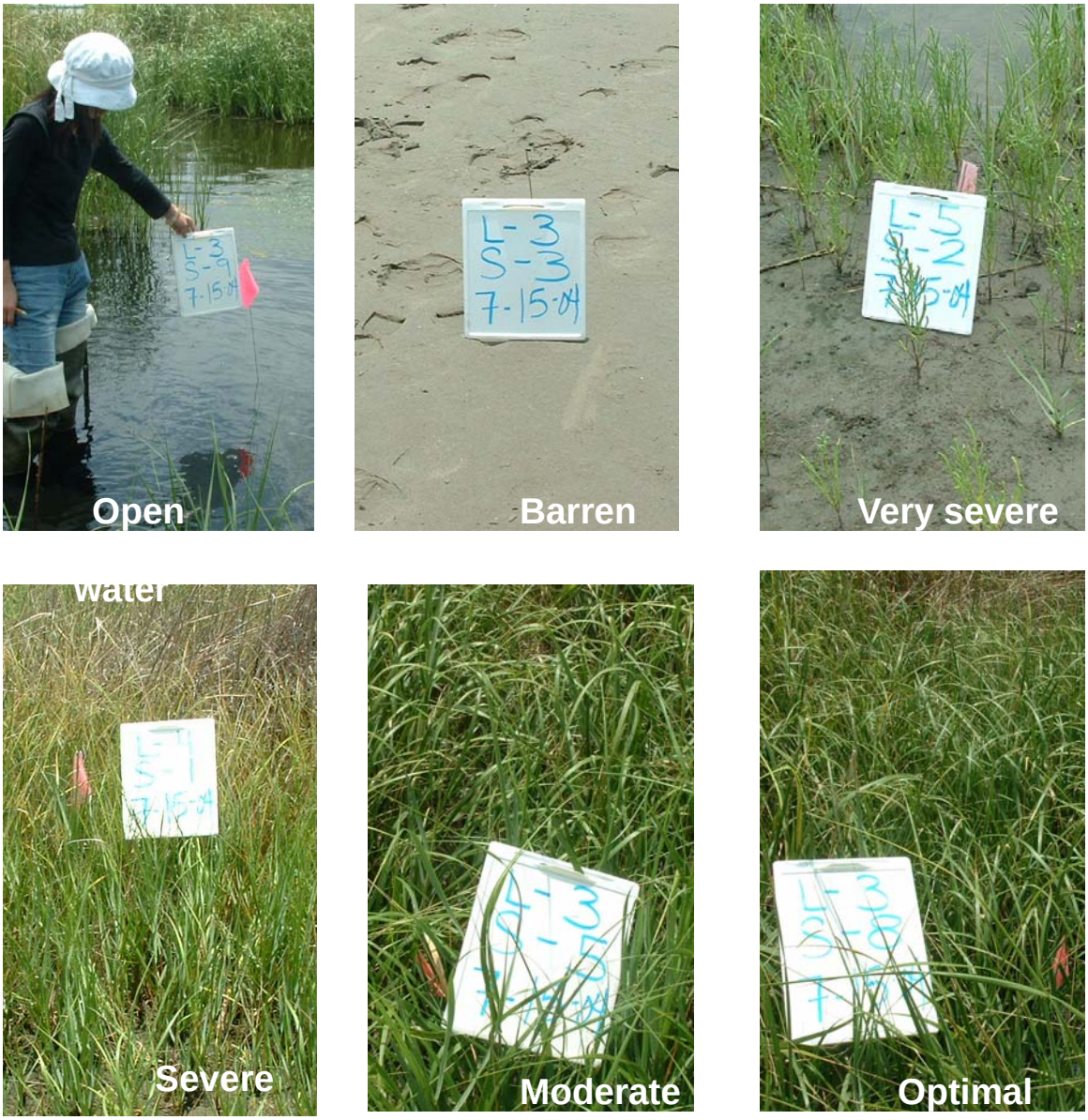

Figure 2-4 Sites were classified into one of six groups based on their relative aboveground biomass and landscape position.

2.3 RESULTS AND DISCUSSION

A wide range in both spatial and seasonal variability was evident within stands of *S. alterniflora* that had voluntarily colonized this marshland within the first year after its reconstruction using from hydraulic dredge spoil from the bottom of a nearby canal. Causal inspection of the reconstructed area shows that while shorelines were often heavily colonized, some shorelines remain barren. Stands tend to diminish as distance from open water and elevations increase, though healthy, highly productive stands occurred at significant distances inland. Efforts to relate plant productivity to elevation, distance from open water, and average daily tidal inundation using multiple regression techniques showed no significant linear or non-linear relationships. To better understand the landscape and edaphic features that contributed to this range of productivity, the 40 monitored sites were classified into one of six categories ranging from optimal to barren based on their relative productivity at time of sampling.

2.3.1 Site Productivity

The amounts of biomass harvested from sites voluntarily stands of *S. alterniflora* averaged 582 g m^{-2} during the course of this study, and ranged from as little as 27 g m^{-2} to 2824 g m^{-2}. An overall decline was evident between the summer and the subsequent spring. Total aboveground biomass in Jul, Nov and Mar averaged 1032, 447 and 246 g•m^{-2}, respectively. The change in harvested biomass between Jul 14 2004 and Mar 25 2005 represented an average decline of 76%. While much of this decline can be attributed to seasonal changes in overall productivity, there is evidence to suggest that other factors

contributed to this decline at some sites. Declines greater than 90% occurred at 10 sites of the 40 sites. Only one site showed a slight increase (18%) between Jul and Mar. None of the barren or open water sites were colonized between April 2004 and March 2005. Figure 2-5 shows the relationship between the amount of living and dead biomass. While the amount of dead tissue tended to increase as the amounts of live tissue increased, the relationship was not strong (r = 0.30), supporting the conclusion that some plots were declining more rapidly than others. When only living biomass was considered, the seasonal decline was somewhat less than the decline in total biomass, and averaged 64% of the living biomass harvested in Jul 2004.

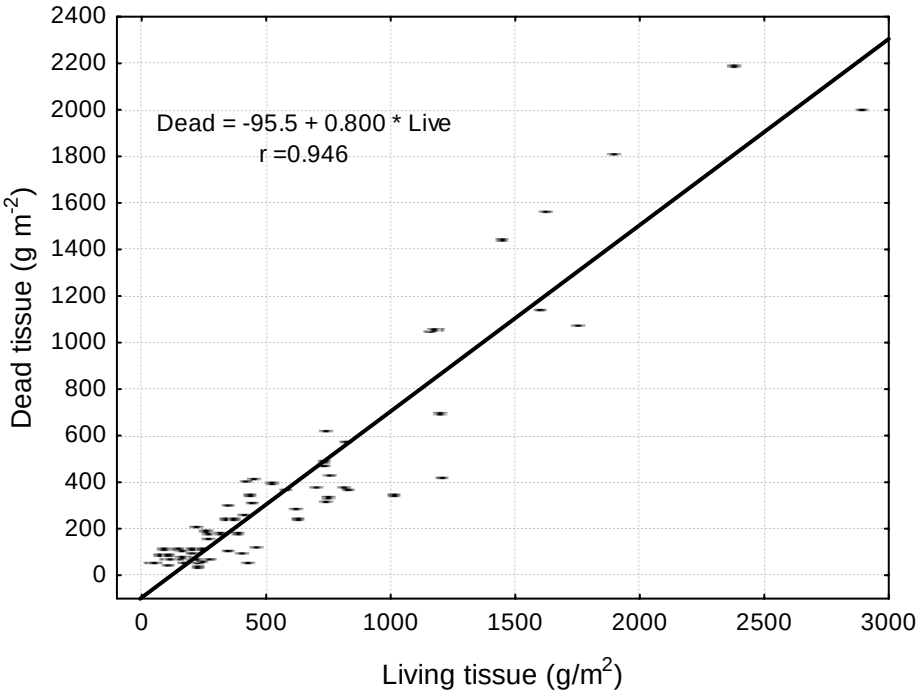

Figure 2-5 Relationship between the amounts of living and dead tissue harvested as above ground biomass between Jul 2004 and Mar 2005

Because some plots appeared to be in decline when the study was initiated, the

productivity of vegetated sites was based on the relative amounts of live biomass present on each sampling occasion (Table 2-2). During mid summer (Jul 2004), optimal sites (> 70% maximum productivity) contained an average of 2382 g m^{-2} of dry tissue. Nearly 85% was living. Moderate sites contained an average of 1602 g m^{-2} of dry tissue and only a slightly less proportion of living tissue (81%). Severe sites not only contained substantially less biomass (834 g m^{-2}), but 38% of the biomass was comprised of dead or dying tissue.

The height of plants growing in sites classified as 'severe' or 'very severe' was substantially reduced. The average mid summer stem height of plants growing in severe environments was only 16.3 cm, whereas the average stem height of plants growing in optimal environments was 40.0 cm (Table 2-2). Plants growing in very severely stressed environments (<15% of maximum living biomass) displayed reduced stem diameter as well as reduced plant height. Although these sites consisted of stunted, sparse plants, a greater portion of the harvested material was living (75%) than in sites classified as severe (38%). This may have been because the 'severe' sites were in more rapid decline, or possibly because the small, thin stems and leaves in 'very severe' site were more easily shed and more rapidly decomposed. It was unclear whether the differences in stem diameters were environmentally induced or due to phenotypic differences within *S. alterniflora*. During initial site selection, an attempt was made to avoid areas where phenotypic differences were clearly evident by the presence of thick-stemmed plants

growing adjacent to shorter, thinner stemmed plants.

Table 2-2 Amounts of aboveground total and living biomass harvested at various times from sites classified on their relative productivity. The average heights and diameters of live stems and the number of living and total stems are also shown. Stem counts were not determined (nd) following harvest in July 2004.

Category	No. sites	Total biomass	Living biomass	Fraction Live	Avg. live stem		No. of stems	
					Height	Diam.	Live	Total
		g•m-2	g•m-2	%	cm	mm	# m^{-2}	# m^{-2}
July 2004								
Optimal	4	2382.0	1979.6	84.9%	40.0	7.2	nd	nd
Moderate	6	1601.8	1280.3	80.8%	26.9	7.4	nd	nd
Severe	9	833.5	546.5	62.0%	16.3	7.0	nd	nd
V. severe	5	244.5	189.1	75.2%	15.2	5.2	nd	nd
Nov 2004								
Optimal	4	1070.0	473.7	44.3%	35.7	5.3	202	345
Moderate	4	693.6	379.3	53.8%	23.8	5.5	143	299
Severe	2	350.8	215.3	61.1%	19.3	5.3	122	214
V. severe	15	109.4	73.9	70.1%	16.3	5.2	112	250
Mar 2005								
Optimal	1	1009.1	320.4	31.8%	36.8	4.9	357	747
Moderate	1	458.0	95.3	20.8%	18.5	3.2	153	317
Severe	15	234.2	58.0	26.0%	22.3	3.9	132	287
V. severe	6	88.8	46.7	56.2%	19.0	4.4	98	272

By late fall (Nov 26 2004), vegetation had senesced in all plots. The average amount of total harvested in Nov was only 43% the corresponding amounts harvested in mid summer. In general, the proportion of dead tissue was greater in the more robust plant stands than in sparsely populated, severely stressed sites. Competition for light and possibly other essential resources no doubt contributed to more extensive senescence in more productive areas. Plant heights in Nov were similar to those in Jul, but a significant reduction in average stem diameter was evident in plants growing in the more favorable environments. Stem diameters of plants growing in optimal or moderate environments

averaged 7.3 mm in Jul, whereas the corresponding diameters of in Nov averaged only 5.3 mm.

Stands of volunteer *S. alterniflora* continued to die back over the winter, but by Mar 2005 a number of new shoots had emerged. Average stem heights were not substantially different from those observed in the preceding seasons, but the average diameter of the young stems was less than those measured in Nov. Only one of the four sites classified as optimal in Jul and Nov remained highly productive throughout the winter. This site was located near the water's edge and warmer rhizosphere temperatures may have helped maintain growth. The other optimal sites were located inland. While they still contained a large number of total stems, most of these stems were dead and had not been replaced with new growth by late March. The lowest proportions of dead stems were found in very severe environments where most of the living biomass, although stunted, appeared to persist throughout the winter.

2.3.2 Influence of Landscape Features

The influence of landscape position on the productivity of *S. alterniflora* in mature coastal wetlands has been extensively studied (Smart 1982, Metcalfe et al. 1986, Collins 2002). In general, stream-side sites support larger, denser populations of *S. alterniflora* than inland sites. In this study, relationships between plant productivity and duration of tidal flooding, and distance from open water were studied using data collected in Jul 2004 when biomass from pioneer stands of *S. alterniflora* were at their maximum.

2.3.2.1 Elevation

Volunteer colonization of *S. alterniflora* occurred at elevations ranging from -7.3 to 37.7 cm relative to MTL (Table 2-3), though plants at the higher elevation were severely stressed. The average elevations of open water sites near the shore line were 11.5 cm below MTL, and those of barren inland sites averaged 22.3 cm above MTL. Among vegetated sites, productivity tended to decrease with increasing elevation. The relationship between elevation and site productivity, however, was not strong. Clearly, other factors also influence volunteer colonization and growth of *S. alterniflora* on this constructed marsh. Six of the most productive sites were located at elevations above the MHW line and the elevation of one of the most productive sites was 30.1 cm above MTL (Figure 2-6). Even so, no *S. alterniflora* was observed growing 8 cm below or 45.3 cm above MTL, suggesting this range can serve as a useful guideline when planning the reconstruction of *S. alterniflora* marsh along the northern Gulf Coast.

Table 2-3 Average elevations relative to mean tide level (MTL) in different environments categorized by their relative plant productivity in Jul 2004. The standard error of the mean as well as minimum and maximum elevations are also shown.

		Elevation relative to MTL (cm)			
Class	No. sites	Average	Std. error	Minimum	Maximum
Optimal	4	14.0	8.6	-2.3	30.1
Moderate	6	13.1	6.4	-7.5	26.7
Severe	9	14.8	3.7	-3.8	33.0
Very severe	5	19.5	6.6	7.1	37.7
Barren	12	22.3	3.2	4.1	45.3
Open water	4	-11.5	2.5	-15.1	-4.1
All	40	14.7	2.4	-15.1	45.3

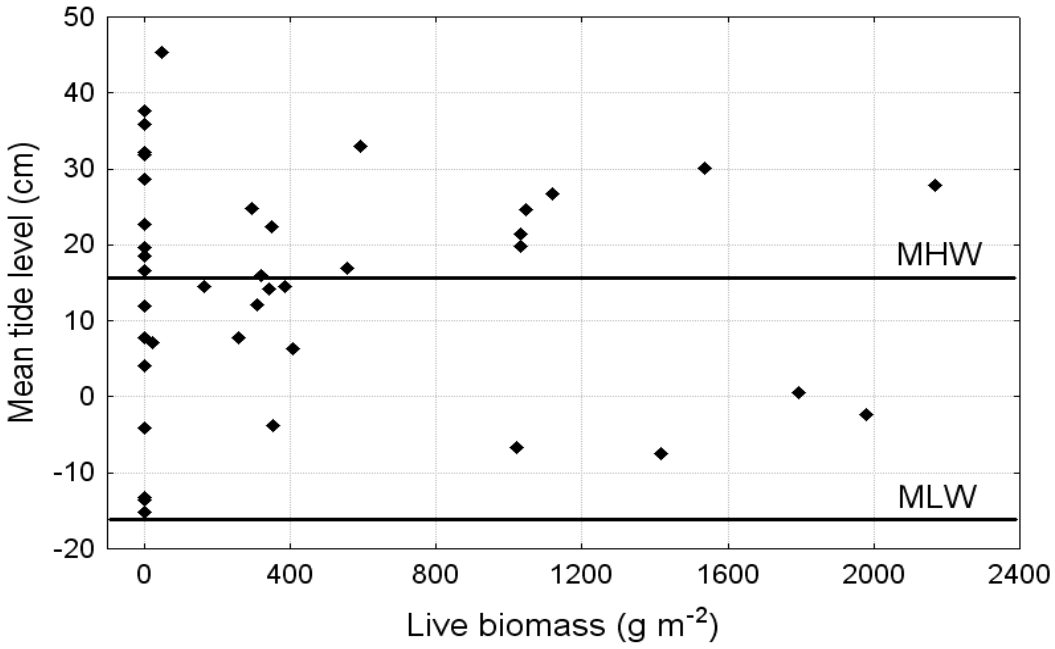

Figure 2-6 Relationship between living biomass harvested in Jul 2004 and site elevation relative to mean tide level (MTL). Mean high water (MHW) and mean low water levels (MLW) are shown.

2.3.2.2 Duration of Flooding

Small differences in elevation can translate into significant differences in the duration of daily tidal flooding along the northern Gulf Coast where the tidal range is generally less that 0.5 m. This is especially true along the gradually sloping shorelines that accrete when hydraulic dredge spoil is discharged during the reconstruction of wetlands. In this study, optimal environments for volunteer colonization were flooded an average of 6.2 hr, but these sites included upland areas 18 cm above the MHW line as well as low-lying shoreline sites that were flooded an average of 13 hrs during each tidal cycle (Table 2-4). No colonization occurred in sites flooded more than 16 hr. It can not be determined from this study whether the failure of extensively flooded sites to colonize

was due to the inability of rafting plants or seeds to become established or because *S. alterniflora* is unable to maintain an adequately aerated rhizosphere in these sediments when tidal flooding exceeded 16 hr per cycle.

Table 2-4 Average duration (hr) of tidal flooding in various environments categorized by their relative plant productivity in Jul 2004. The standard error of the mean as well as minimum and maximum hours of flooding are also shown.

		Avg. duration of tidal flood(hours)			
Class	No. sites	Average	Std. error	Minimum	Maximum
Optimal	4	6.2	3.6	0.0	13.1
Moderate	6	5.2	3.3	0.0	15.9
Stress	9	4.4	1.7	0.0	13.9
Severe stress	5	3.0	1.6	0.0	8.5
Barren	12	2.0	1.1	0.0	10.1
Open water	4	18.8	1.7	14.0	21.7

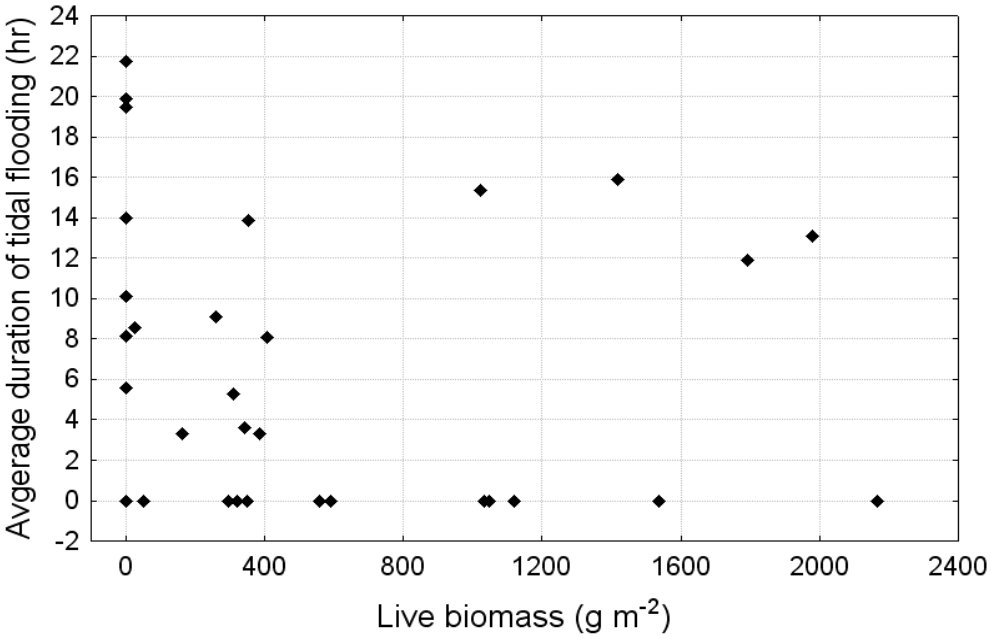

Figure 2-7 Relationship between live biomass (Jul 2004) and average duration of tidal flooding.

The productivity of vegetated sites tended do decrease as flooding duration

decreased, but as with elevation, other mitigating factors clearly played a role in determining both colonization and over all productivity. Figure 2-7 shows that more productive sites were clustered along shorelines inundated from 12-16 hr per cycle, or in upland sites that were seldom flooded except during storm events. Vegetated sites within the upper tidal zone inundated 2-12 hrs per cycle generally had lower levels of productivity than shoreline sites and the five most productive sites above MHW.

2.3.2.3 Distance From Open Water

Table 2-5 Distance from open water of various environments categorized by their relative plant productivity in Jul 2004. The standard error of the mean as well as minimum and maximum distances of each category are also shown.

		Distance from open water (m)			
Class	No. sites	Average	Std. error	Minimum	Maximum
Optimal	4	19.1	10.0	1.7	42.0
Moderate	6	18.6	8.8	1.4	59.7
Severe	9	27.4	8.4	1.7	72.4
Very severe	5	17.4	6.1	1.0	36.0
Barren	12	28.0	5.7	0.0	65.1
Open water	4	-1.8	0.6	-2.9	-1.0

The clear relationship between distance from the stream edge and productivity of *S. alterniflora* commonly observed in mature marsh was not evident among plants growing at this reconstructed site (Table 2-5). While two of the optimal sites were located near open water, equally productive sites were found as much as 42 m inland. Stunted stands were found as far as 72 m inland, though it is possible that other volunteer stands not included in the study areas were located at greater inland distances. The data in Figure 2-8 indicates that close proximity to water sites within 20 m of open water did not ensure colonization success. Efforts to establish relationships between productivity and

elevation or flood duration and distance from open water using multiple regression techniques showed no significant relationships. Clearly, factors other than landscape position are important in determining the success of volunteer colonization of reconstructed areas.

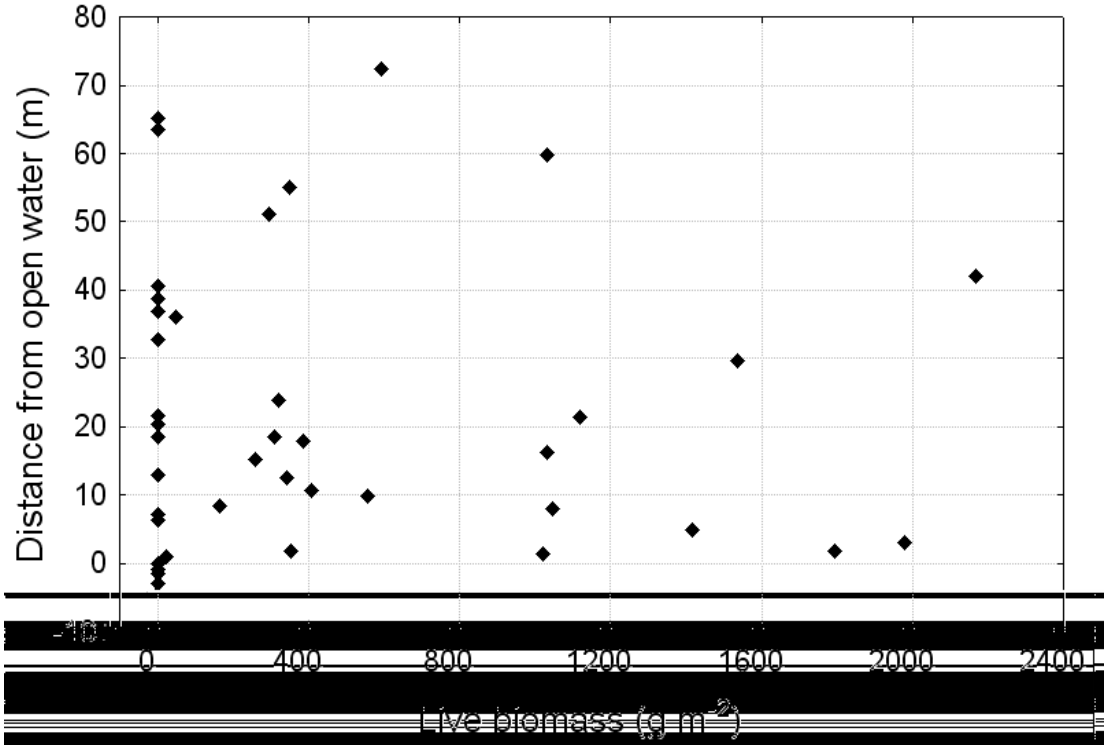

Figure 2-8 Relationship between live biomass (Jul 2004) and distance from open water.

2.3.3. Tissue Analyses

Comparisons of nutrient uptake in plants collected from sites with various levels of productivity indicated that *S. alterniflora* harvested from 'severe' or 'very severe' environments tended to be lower in N and K than more productive sites (Table 2-6). The C: N ratios in the most severely stressed sites averaged 51 whereas those in the most productive sites averaged 38 were total N uptake was 10 times greater (Table 2-6). The

Table 2-6 Concentrations of essential and potentially toxic elements in living aboveground *S. alterniflora* tissue harvested from sites of varying productivity.

Element	Units	V. severe	Severe	Moderate	Optimal	Optimal Jul 2004
Major nutrients						
N	g kg^{-1}	8.40a	9.52ab	10.06b	10.53b	10.17
P	mg kg^{-1}	1975	1882	1700	1872	1098
K	mg kg^{-1}	6631a	7141ab	8768b	8299b	9561
Secondary nutrients						
Ca	mg kg^{-1}	3343	3389	2941	4127	3661
Mg	mg kg^{-1}	3597	3914	3034	3736	2482
Na	mg kg^{-1}	24546	26303	21591	25525	12269
S	mg kg^{-1}	4627	4917	4142	4633	3483
Al	mg kg^{-1}	624a	552a	322b	324b	134.8
As	mg kg^{-1}	5.80	5.06	5.45	4.76	6.8
B	mg kg^{-1}	13.3	14.9	10.7	13.1	12.3
Cd	mg kg^{-1}	0.9	1.0	1.2	1.5	3.8
Cu	mg kg^{-1}	4.8	5.4	4.7	5.2	6.4
Fe	mg kg^{-1}	615a	561a	281b	324b	147.3
Mn	mg kg^{-1}	126.2	155.5	111.4	120.3	151.9
Mo	mg kg^{-1}	4.0	3.3	3.9	3.9	9.4
Ni	mg kg^{-1}	18.4	19.2	12.0	15.6	4.5
Se	mg kg^{-1}	8.0	8.2	8.1	7.0	13.7
Zn	mg kg^{-1}	37.7	43.0	33.7	37.5	31.0

Values represent the averages of plants collected in Jul, Nov. and Mar. Concentrations followed by different letters were significantly different ($p<0.05$) between environments importance of N and P uptake in the success of volunteer colonies of *S. alterniflora* will be discussed more fully in Chapter 3. Tissue concentrations of K tended to increases with increasing site productivity. While critical tissue concentrations have not been established for K or most other essential nutrients, the clear relationship between site productivity and tissue K concentrations strongly suggest that limited K availability is a factor

influencing productivity of *S. alterniflora* in coastal wetlands reconstructed from dredge spoil.

No significant differences among environments were observed in tissue concentrations of secondary nutrients, though concentrations of Ca, Mg and Na were significantly greater in tissue harvested in late fall and winter than in summer. In Nov. 2005, tissue concentrations of Ca, Mg and Na averaged 1.5, 1.8 and 2.4 times greater than in plants harvested in Jul 2004. It is noteworthy that the molar ratio of Ca to Mg averaged only 0.58. The relationship between Ca, Mg, and Na in wetland plants has not received the level of attention that has been devoted to upland plants, and therefore it is difficult to interpret the importance of low Ca uptake relative to that of other cations in S. alterniflora. The low uptake of Ca was presumably due to the low ratio of Ca to Mg in the saline waters of the northern Gulf Coast, and its possible *S. alterniflora* has adapted to this common condition. A greater Ca to Mg ratio was observed in Jul than in Nov or Mar, suggesting that Ca was selectively lost in senescing tissue or that the ability of the sediments to supply Ca decreased. Concentrations of Na, Fe, and Al, elements that can adversely affect plant growth were all much lower in the standing biomass harvested from optimally productive sites in Jul than in Mar and Nov. These findings suggest that the availability of both essential nutrients and potential toxins is greater in summer than in the cooler months.

Tissue concentrations of Al and Fe were significantly greater in the more severely

stressed sites than in the more productive areas (Table 2-6). The concentrations of Al averaged 624 mg/kg in the most severely stressed plants and averaged only 324 mg/kg in the most productive plants. Similarly, Fe averaged 615 mg/kg in severely stressed plants and only 324 mg/kg in the most productive sites. Maximum levels of tolerance for Al and Fe have not been established for *S. alterniflora*, but the concentrations observed exceed the tolerance limits of most crops. For example, the maximum tolerance levels of Al and Fe in rice are 200 and 500 mg/kg, respectively (Benton et al., 1991). Excessive uptake of Fe by wetland plants is linked to the increased availability of these nutrients in soil and a diminished ability of wetland plants to oxidize highly soluble forms of these metals on their root surfaces.

Table 2-7 shows the accumulations of various nutrients in aboveground standing biomass averaged over summer, fall and winter. Statistical differences are not indicated because most differences can be attributed to differences in biomass. Plant uptake of N, P, and K in the most productive sites averaged 155, 28, and 122 kg/ha, respectively. In Jul 2004 when aboveground biomass production was near its annual optimum, the amounts of N, P, and K assimilated in the most productive sites averaged 229, 24, and 210 kg/ha. It is noteworthy that assimilation of both N and K were significantly higher in Jul than their annual averages, whereas P uptake showed a slight decrease. In Jul, optimal stands contained 80, 54 and 76 kg/ha of Ca, Mg and S, respectively. This accumulation of Ca is low in comparison to non-halophytes, and the amount of S is high. These stands

contained 269 kg Na/ha, raising the possibility that Ca availability may be a limiting factor in this reconstructed wetland. This possibility is supported by the observation that Ca tissue concentrations were lower in less productive sites. Also, a reduction in the amount of assimilated Ca and a marked increase in the assimilation of Na was observed between Jul and Mar in all sites, especially those that showed the most declines in biomass over this period.

Table 2-7 Total amounts of various nutrients assimilated on a per hectare basis by standing *S. alterniflora* biomass harvested from sites of varying productivity. Values represent the averages of plants collected in Jul, Nov. and Mar. 'Maximum assimilated' represents the amounts of various nutrients in Jul 2004 in stands showing optimal growth.

Element	Units	Very severe	Severe	Moderate	Optimal	Optimal Jul 2004
Major nutrients						
N	kg ha^{-1}	15.9	35.9	108.1	154.9	222.9
P	kg ha^{-1}	3.7	7.1	18.3	27.5	24.1
K	kg ha^{-1}	12.6	26.9	94.2	122.1	209.5
Secondary nutrients						
Ca	kg ha^{-1}	6.3	12.8	31.6	60.7	80.2
Mg	kg ha^{-1}	6.8	14.7	32.6	54.9	54.4
Na	kg ha^{-1}	46.5	99.1	232.1	375.4	268.9
S	kg ha^{-1}	8.8	18.5	44.5	68.1	76.3
Trace elements						
Al	g ha^{-1}	1181	2081	3464	4771	2954
As	g ha^{-1}	11	19	59	70	148
B	g ha^{-1}	25	56	115	193	271
Cd	g ha^{-1}	2	4	13	22	84
Cu	g ha^{-1}	9	20	51	76	140
Fe	g ha^{-1}	1165	2113	3025	4771	3229
Mn	g ha^{-1}	239	586	1197	1769	3329
Mo	g ha^{-1}	8	12	42	58	207
Ni	g ha^{-1}	35	72	129	229	99
Se	g ha^{-1}	15	31	87	103	299
Zn	g ha^{-1}	71	162	362	552	679

2.3.4. Edaphic Factors

The physicochemical properties of sediments associated with various levels of productivity were examined in an attempt to identify factors that may account for differences that could not be attributed to landscape position or nutrient uptake. Edaphic factors may also account for those sites that remained barren for 24 mo after marsh construction even where landscape position was favorable for growth.

The importance of the physiochemical substrate properties in determining colonization was demonstrated in a simple experiment where eight vigorous *S. alterniflora* plants were collected in Apr 7, 2004, trimmed to a height of 12", and transplanted to an adjacent barren area near the MHT line. A site visit in early Jun about six weeks after transplanting showed all of the aboveground portions had declined and showed no signs of new growth. In Jul, it was clearly evident that both the above and below ground portions were dead.

2.3.4.1 Salinity

Salinity has been found to have a marked influence on the productivity of *S. alterniflora* in natural coastal marshes (Nestler 1977) where elevated osmotic potential reduces water availability and high levels of Na and Cl can inhibit N uptake and adversely affect membrane integrity and overall metabolic function (Linthurst and Seneca 1981, Pezeeshki and Delaune 1993).

The electrical conductivity (ECse) of the underlying sediments in sites supporting optimum productivity of volunteer *S. alterniflora* average 11.7 dS m^{-1}, and was only

slightly greater in vegetated sites with the lowest levels of productivity (Table 2-8). The ECse of open water sites was only slightly greater than those of vegetated sites and it is unlikely that this difference in salinity accounts for the fact that open water sites failed to colonize.

In contrast, the ECse of inland barren sites (27.6 dS m^{-1}) was 2.3 times that of vegetated sites. Greatly elevated ECse is the most evident difference between vegetated and barren sites, and may account for the fact that these sites show no evidence of colonization by *S. alterniflora* or any wetland species for 24 mo after marsh construction. Visual examination of barren in spring and summer showed that many of the barren areas near MHW had accumulated generous amounts of seed. The failure of this seed to germinate may be attributed, at least in part, to the fact that average ECse in barren sites greatly exceeded the levels where *S. alterniflora* seed can germinate and grow (Wijte and Gallagher, 1996a, b).

It is difficult to account for the higher levels of salt in the sediments of these barren since they occupied a range of landscape positions including several sites below the MHT level. At higher elevations, evaporation from the sediment surface and the deposition of salt spray may contribute to elevated salt concentrations. The high salinity levels at lower elevations may be an artifact of initial marsh construction. While it is possible that the initial sediments deposited contained higher levels of salt, it is more likely that slight variations in local topography created drainage paths during and after

pumping. The lower amounts of organic matter and clay in the barren areas are consistent with the hypothesis that these areas currently or once served as drainage areas. Once deposition of hydraulic dredge spoils ceased, flow generated by subsequent rainfall events may have been insufficient to flush salts into open water, causing salts from upland areas accumulate to a degree that colonization is prevented.

Table 2-8 Average annual values for physiochemical properties of sediments in supporting various levels of productivity. Values followed by different letters were significantly ($p < 0.05$) different.

Class	pH	ECse	Moisture	Org. matter	% Sand	% Clay	% Silt
		dS m^{-1}	g H_2O g^{-1}	g kg^{-1}	g kg^{-1}	g kg^{-1}	g kg^{-1}
Optimal	8.02	11.7a	0.28a	19.7b	425a	53a	522a
Moderate	8.04	9.9a	0.28a	19.9b	481b	62a	458a
Severe	7.81	11.6a	0.30a	16.4b	385a	119b	497a
V. severe	7.77	12.8a	0.27a	13.1ab	503b	45a	452a
Barren	7.75	26.7b	0.24a	10.5a	538b	30a	432a
Open water	7.94	14.4a	0.35c	27.2c	323c	93ab	583b

2.3.4.2. Textural Characteristics

The mineral textures of sediments ranged from loam to silt loam. Sediments supporting optimal productivity contained and average of 43% sand, 52% silt and 5% clay (Table 2-8). Few significant differences were evident, though sites classified as ‘severe’ containing higher amounts of clay than did more productive sites, and sites classified as ‘very severe’ or ‘barren’ contained higher amounts of sand. Organic matter levels were higher in the more productive vegetated sites. The organic matter content of barren sediments was approximately half that of the most productive sites, and undoubted influenced the ability of these sediments to supply water and nutrients.

It is noteworthy that the sediments in areas classified as 'severe' contained significantly more clay and less sand than more productive or barren areas. These differences suggest that sediments in the 'severe' areas were comprised of different parent materials or served as catch basins during marsh construction. Sediments in open water sites also contained more clay and silt as well as significantly more organic matter than sites above the vegetated shoreline, possibly due to accumulation of eroded sediments from higher elevations. The composition of the sediment solids appeared to exert little influence on their average moisture content. On all sampling occasions, moisture contents were near saturation. The exceptionally high electrical conductivities measured in the persistently barren sites may have exerted sufficient osmotic potential to reduce water availability in those sites.

2.3.4.3. Eh, Sulfide and Available Metals

Tidal flooding and the shallow water table in coastal wetlands reduce diffusion of atmospheric O_2 into sediments. However, *S. alterniflora* is similar to many other wetland plants in its capacity to partially oxidize its rhizosphere by translocation of O_2 from its leaves to roots via specialized parenchyma cells, leading to oxidation of $Fe^{2+}$and Mn^{2+} on or near root surfaces (Madureira et al. 1997, Sundby et al. 1998). Even so, oxidation-reduction reactions in saturated sediments can yield potentially toxic concentrations of sulfide, reduced iron and other compounds. Howes et al. (1986) concluded that *S. alterniflora* growth is more closely related to the extent of sediment oxidation than to available N or interstitial salinity.

In highly reduced sediments, sulfate is reduced to sulfide by microorganisms capable of using sulfate as an alternative electron acceptor. Typical seawater contains 2.6 mg SO_4^{-2} L^{-1} (Turekian, 1968), and therefore its supply can be considered unlimited in sediments frequently inundated in coastal marshes. It has been suggested that sulfide is the major factor limiting the growth of coastal marsh plants, though the adverse effects of sulfide are strongly influenced by sediment drainage, sulfide concentration and ferrous iron concentration (King et al. 1982, Osgood and Zieman 1993). Sulfide is highly reactive with metals such as ferrous iron and forms insoluble precipitates that reduce the activity and toxicity of sulfides.

In the study reported here, few differences were found in average Eh levels or concentrations of available sulfide, iron or other metals among sediments supporting various levels of productivity. The most notable differences were between open water sites and vegetated sites occupying higher landscape positions (Table 2-9). Average annual sulfide concentrations in pore water ranged from 3.0 to 3.4 mM L^{-1}. These levels exceed the maximum concentration of 1 mM L^{-1} found optimal in a greenhouse study (Morris et al. 1996), but are less than the 7 mM reported by Carlson and Forrest (1982) in a North Carolina salt marsh. While average sulfide concentrations in Jul ranged from 4.2 to 5.8 mM L^{-1} and were 2 to 2.3 times those at other times of the year, the highest levels of sulfide were invariably observed within the sediments supporting the highest levels of productivity, suggesting that either the concentrations observed were within the tolerance

range of *S. alterniflora* or other factors mitigated the toxicity of sulfide in this recently constructed marsh.

The prolonged tidal flooding at open water sites is reflected in their lower average redox (Eh) potentials and higher levels of DTPA-extractable iron (Fe) and manganese (Mn). DTPA is a chelate commonly used to assess plant availability of trace metals in soils and sediments. The amounts of DTPA-extractable Fe was lower in barren areas than in vegetated areas, but it is uncertain whether low iron availability contributed to the inability of barren sites to support colonization. Tissue concentrations of Fe were much greater in 'very severe' and 'severe' than in more productive sites, yet sediments in the severe environments contained the lowest amounts of extractable Fe. Stunted growth due to high salinity levels may result in plants that lack sufficient leaf area to adequately oxidize their rhizospheres by translocation of O_2 within the plant and thereby prevent uptake of soluble Fe by precipitation on or near root surfaces.

Table 2-9 Eh, sulfide in pore water and DTPA-extractable metals in sediments supporting various levels of productivity. Values followed by different letters were significantly ($p < 0.05$) different.

			DTPA extractable			
Class	Eh	Sulfide	Cu	Fe	Mn	Zn
	Mv	Mmol S L^{-1}		mg kg-1		
Optimal	68.4a	3.39	0.54	36.0a	6.73a	1.30
Moderate	34.7a	3.44	0.50	32.7a	6.30a	1.36
Severe	27.4a	2.91	0.75	31.6a	9.66ab	2.12
V. severe	46.4a	3.00	0.52	33.4a	9.84ab	1.68
Barren	70.0a	3.05	0.45	21.0b	5.92a	1.31
Open water	-35.8b	3.29	0.94	48.9c	13.6b	1.18

2.3.4.4. Exchangeable Cations and CEC

Table 2-10 Average cation exchange capacity (CEC), exchangeable cations, Ca to Mg ratio and exchangeable sodium percentage (ESP) of sediments supporting various levels of productivity. Values followed by different letters were significantly ($p < 0.05$) different.

Class		Exchangeable cations					
	CEC	Ca	Mg	K	Na	Ca:Mg	ESP
	meq^{+} 100 g^{-1}			mg kg^{-1}		ratio	
Optimal	29.4a	147.2a	57.2a	32.0a	379.3a	1.6a	56.2%a
Moderate	22.7b	111.6b	46.6a	27.7a	289.7a	1.5a	55.5%a
Severe	27.3ab	103.9b	59.4a	28.2a	379.8a	1.1b	60.5%ab
V. severe	24.7a	91.9b	50.9a	28.8a	349.6a	1.1b	61.5%b
Barren	20.5a	87.5b	44.1a	20.4b	274.9a	1.2b	58.4%ab
Open water	38.9c	166.5a	78.4b	41.2c	532.0c	1.3ab	59.4%ab

The average cation exchange capacity (CEC) of sediments supporting optimal growth was somewhat greater than those of other vegetated sites, consistent with the higher amounts of organic matter in optimal sites (Table 2-10). Open water sites, which contained the greatest accumulation of organic matter and clay, displayed the highest CEC, whereas the lowest average CEC was found in persistently barren sites above the shoreline. The ratio of calcium to magnesium (wt/wt) was greater in the more productive sediments. This finding is consistent with the fact that the plant tissue of more productive areas contained a more favorable balance of Ca to Mg and K to Na. The influence of Ca and Mg ratios on growth of *S. alterniflora* has not been extensively studied, but a similar positive relationship between K concentrations in sediments and growth of *S. alterniflora* was reported by Delaune and Pezeshki (1988). The exchangeable sodium percentage (ESP) tended to decrease with increasing productivity, though these differences were not

large. The ESP of 'optimal' sites was 56.5% whereas that of the sites classified as 'very severe' averaged 61.5%. ESP of persistently barren sites was similar to marginally productive sites, suggesting that the principal differences in salinity among these sites lies in the much greater electrical conductivity in barren sites, and not to the propotion of Na present.

2.3.4.5. Total Elemental Composition

Non-vegetated open water sites contained significantly ($p < 0.05$) greater concentrations of Al, Fe, K, Mg, Na and S than sites higher in elevation (Table 2-11). Few differences were found among vegetated sites, though the more productive sites tended to contain lower amounts of Na and Al. The similarities among vegetated sites suggest that parent materials did not differ significantly among sites supporting different levels of productivity. Large differences would not be expected since the floatation canal that served as the source of sediments was dredged to a consistent depth and the dispersal of hydraulic spoil results in extensive mixing.

Table 2-11 Average total concentrations of selected elements found in sediments supporting various levels of productivity. Values followed by different letters were significantly ($p < 0.05$) different.

Class	Al	Ca	Fe	K	Mg	Mn	Na	P	S
				mg kg^{-1}					
Optimal	6506a	6859	15338a	1817a	5329a	728	4130a	360	3746a
Moderate	6754a	5593	13741a	1641a	5974a	972	4145a	347	3617a
Severe	8680b	7334	18804a	2326a	6815a	574	6163b	408	3180a
V. severe	8046ab	7633	15593a	1914a	6187a	755	5994b	391	2636a
Barren	6906a	7358	14309a	1824a	6187a	597	6441a	370	2425a
Open water	9170b	7759	30441b	3212b	8069b	828	7577c	439	6535b

2.4 CONCLUSIONS

The clear relationship between landscape position and productivity of *S. alterniflora* that is commonly observed in natural marshes was less evident among volunteer stands growing on constructed marsh. No volunteer stands were observed growing 8 cm below or 45.3 cm above MTL, though six of the more productive sites were located at elevations above the MHW line and the elevation of one of the most productive sites was 30.1 cm above MTL. Highly productive sites were found along shorelines and as far as 42 m inland. No stands of *S. alterniflora* were found more than 72 m from the waters edge, even in low-lying areas. It possible that seed or vegetative propagules are not distributed great distances inland, and that some of the barren inland sites may eventually support *S. alterniflora* or other coastal vegetation. Optimal environments were flooded an average of 6.2 hr d^{-1}, but highly productive sites included low-lying shoreline sites that were flooded an average of 13 hrs during each tidal cycle as well upland areas 18 cm above the MHW line that were seldom flooded. No colonization occurred in sites flooded more than 16 hr during an average tidal cycle. All vegetated sites displayed optimal growth in Jul, and shed a significant portion of their aboveground biomass by Nov. Some sites appeared to be in more rapid decline than others, especially in environments classified as 'severe' at the initiation of this study. This decline may have been due to subtle changes in elevation as sediments continued to de-water after initial construction with hydraulic dredge spoil. None of the sites found barren at the initiation of the study were colonized between Apr 2004 and Mar 2005. Attempts to plant barren

areas with vigorous, freshly-collected plants resulted in failure.

Plants harvested from highly productive areas contained more N and K and less Fe and Al than did those harvested from less productive areas. The possibility excessive uptake of Fe or Al adversely affects growth of *S. alterniflora* on constructed marsh merits further study. Low turnover in the least productive areas suggest they do not have a significant impact on nutrient cycling in this marsh ecosystem. Fertilization with a blended fertilizer would likely improve productivity except in the least productive sites where growth is clearly limited by high soil electrical conductivity and other factors. More productive sites contained more organic matter and lower amounts of salts than less productive sites. The failure of barren areas to colonize appears to be due primarily to accumulation of excessive level of salts that prevent seed germination or growth of rafted plants. The cause of salt accumulation in these areas can not be known with certainty, but it appears that barren areas currently or once served as drainage areas with insufficient sheet flow to flush salts into open water. Regardless of the cause, construction of narrow drainage ditches would facilitate the flushing of salts and volunteer colonization of barren areas at elevations capable of supporting *S. alterniflora.*

CHAPTER 3 RELATIONSHIPS BETWEEN NITROGEN AND PHOSPHORUS UPTAKE AND GROWTH OF VOLUTEER S. ALTERNIFLORA IN A RECONSTRUCTED WETLAND

3.1 INTRODUCTION

Nitrogen (N) has been identified as a major factor limiting the growth of *S. alterniflora* in intertidal areas. Inadequate supplies of nitrogen are likely to affect overall wetland function by altering the basic ecosystem processes of productivity, decomposition and food chain support (Langis et al. 1991, Valiela, 1983). It is reasonable to assume that the relationship between nitrogen uptake and production *of S. alterniflora* is similar to that in other ecosystems where uptake is influenced directly by nitrogen availability in soils or sediments.

Several studies have demonstrated that nitrogen (N) fertilizer applications increase both tissue N and yield in *S. alterniflora*, and therefore it is often assumed that the productivity of natural stands is N limited. Patrick and Delaune (1980) found a significant growth response of *S. alterniflora* to added nitrogen but not phosphorus at a streamside location in a Louisiana marsh. A greater response to applied nitrogen was found at inland sites than at streamside locations. Osgood and Zieman (1993) also reported significant increase in mean height and increased biomass after N fertilization. These findings support the conclusion of Valiela et al. (1982) that the shorter forms of *S. alterniflora* found in the interiors of coastal marshes are principally determined by nitrogen supply.

Less is known regarding the fertility of constructed wetlands where the substrate

composition varies depending on the sediment source. Typically, soil N is highly positively correlated with soil organic carbon levels. The low amounts of organic matter in dredge spoil may not be sufficient to support optimal vegetative growth in salt marshes reconstructed from these materials (Lindau and Hossner 1981, Craft et al. 1986, Langis et al. 1991). Lindau and Hossner (1981) compared substrate nutrients levels in constructed and natural marshes on the coast of Texas. Their natural wetland had low soil organic carbon (<1.3% soil dry mass) and nitrogen content (total N< 600 mg/ kg), but levels in the constructed marsh were even lower (<0.5% dry mass and < 100 mg/kg, respectively), though the amounts of available N and P increased during the 16-mo study. Craft et al. (1986, 1988a) compared total nitrogen, phosphorus, and organic carbon pools in natural and transplanted marsh soils of the North Carolina coast. In the most if the natural marshes they studied, organic carbon and nutrients were higher than in the transplanted marsh soils. Covin and Zedler (1988) found that one-time additions of urea in a newly constructed marsh at San Diego Bay increased the height of *S. alterniflora*. However, the rate of urea application may not have been sufficient in that study as it failed to produce *S. alterniflora* as tall as those in nearby natural marshes.

Phosphorus availability in wetlands is controlled by complex *in situ* biotia and abiotic processes. These processes within the chemical environment of the sediments are influenced by the mineral composition, pH, and redox conditions (Jugsujinda et al. 1995, Jones et al. 1993). When soil pH is high (7-8), the usual case for most salt marsh soils,

calcium phosphate is a dominant form of inorganic P and is largely unavailable for plant uptake (Broome et al. 1975, Olff et al. 1993). Other forms of phosphorus iron and aluminum phosphates, are more soluble in the anoxic, high pH conditions found in coastal marshes, and therefore are more available for plant uptake (Broome et al. 1975). During natural salt marsh development, clay is deposited on the marsh surface. Clay minerals contain P and can also increase the amount of available P by promoting reducing conditions in the rhizosphere (Olff et al. 1997). Phosphorus limitation at the early successional stage in naturally accreting wetlands has been attributed to relatively low clay content (Olff et al. 1997, van Wijnen and Bakker 1997). In contrast, P limitations are less likely in mature marsh where appreciable amounts of clay minerals have accumulated. Even so, it is generally assumed that when nitrogen supply is sufficient in coastal wetland, phosphorus becomes limiting (Cargill and Jefferies 1984).

The primary objectives of the studies reported in this chapter are (1) to assess whether N or P availability influence the productivity of volunteer *S. alterniflora* on marshland constructed from dredge spoil and (2) to determine the amounts of N and P assimilated in stands of optimal productivity. Changes in seasonal uptake and relationships between soil N fractions and N uptake are also examined.

3.2 MATERIALS AND METHODS

This study was conducted near Port Fourchon LA (29º08' N, 90º12' W) in a coastal wetland reconstructed using spoil generated by hydraulic dredging of a nearby

floatation canal. Transects were established in each stand and sites were selected along these transects to reflect the range of plant productivity. The first transect (T1) was located in a low-lying area at the end of a shallow bay lying just inside of the small levee that divided the constructed area from the adjacent flotation canal. This transect originated in open water ~2 m from nearest shoreline vegetation and ranged inland 2 m beyond the point where *S. alterniflora* ceased to grow. The second (T2) and third (T3) transects were similar but located at somewhat more sharply sloping areas along the bay. The fourth transect (T4) originated at a small tidal stream that traversed the area. The fifth stand was located in the interior of the reconstructed area and a transect (T5) originated in a small cut that opened directly into the floatation canal and traversed low-lying areas containing lush stands and devoid of vegetation similar elevations. Sampling sites were established along each transect to represent a range of biomass productivity. A total of 40 sampling sites were selected along the gently undulating slopes of these transects.

3.2.1 Plant Samples Analysis

In April 2004, the uppermost fully expanded leaves were collected from 10 plants for elemental analysis. On subsequent sampling occasions beginning in Jul 2004, plant samples were harvested in addition to leaf samples by cutting all plants within a 0.3 m^2 area at ground level. Plant samples were placed in plastic litter bags for transport to the laboratory where they were sorted into living (>50% green tissue) and dead *S. alterniflora,* and dead material was discarded. Individual plants were separated into stems

and leaves. The material was dried to a constant weight at (65^{o}C; 48h) for analysis of C, N, and P contents. The percent carbon and percent nitrogen in whole plants and leaves were determined by dry combustion using an automated CN analyzer (Carlo Erba FlashEA 1112). The percent of phosphorus was determined by ICP (Perkin-Elmer model 1100B) analysis of HNO_3: HCl acid digests (3: 1) of dried, finely ground plant samples (0.5 g).

3.2.2 Soil Samples Analysis

Bulk surface samples (0-15 cm) of sediment were also collected in each harvested quadrant. Approximate 1 L of sediment from each site was placed in a 4-mil Ziploc™ bag (20 x 25 cm), the air squeezed from bag before sealing, and the sample place on ice for transport to the laboratory for analysis. Samples were dried (65^{o}C; 48 h) and crushed to pass a 2-mm screen for determination of elemental composition. Soil analyses consisted of measurements of total and available contents of C, N and P. Organic C and total N were determined by dry combustion using a FlashEA 1112 NC analyzer. Concentrations of ammonium and nitrate (dissolved inorganic nitrogen) were determined in pore water expressed from a sub-sample of sediment from each site after filtering through a 0.45 μm filter. NH_4^+ was determined by an automated membrane diffusion technique using an Alltech Ammonia Analyzer. To determine NO_3^-, the instrument was fitted with a Zn reduction column to quantitatively reduce NO_3^- to NH_4^+. Concentrations of NO_3^- were calculated as the difference between measurements with and without the use of a Zn column. The instrument was calibrated with ammonium nitrate standards before

use and recalibrated after every 20 samples. Soil available phosphorus was measured by NH_4F and HCl (1:2) method of Bray and Kurtz (1945).

3.2.3 Statistics Analysis

To identify relationships between plant productivity and environmental factors, data were explored using both multivariate and ANOVA analyses. For the later, sites were classified into one of six microenvironments. Vegetated sites were classified as ‘optimal’ if they supported between 70% and 100% of the maximum live biomass measured on each sampling occasion. Similarly, sites were classified as 'moderate' if they contained between 45% and 70% of the maximum live biomass, ‘severe’ between 15% and 45%, and 'very severe' if they contained between 1% and 15% of the maximum live biomass at time of sampling. Non-vegetated sites with elevations greater than the vegetated shoreline were classified as 'barren' whereas non-vegetated sites with elevations less than the nearby shoreline were classified as ‘Open water’. One-way analyses of variance (ANOVA) were used to test for a significant difference among the grouped sites. ANOVA followed by the Duncan multiple range test (SAS 1996) was used to identify significant differences ($P \leq 0.05$).

3.3 RESULTS AND DISCUSSION

3.3.1 N Assimilation

N concentrations ranged from 9.63 g kg^{-1} in the uppermost fully expanded living leaves of volunteer *S. alterniflora* collected in Jul from very severe environments to as much as 18.2 g N kg^{-1} in the corresponding leaves collected from moderate environments

the preceding April (Table 3-1). Leaf tissue N was greatest in Apr 2004 when the average of all sites was 15.6 g N kg^{-1}. By Jul 2004, average leaf N concentrations had declined to 10.8 g N kg^{-1}. This decline was most evident in very severely stressed environments where concentrations decreased from 14.8 to 9.6 g N kg^{-1} during this 3-month period when climatic conditions favored rapid growth. While analysis of uppermost leaves has the advantage of offering a non–destructive means of monitoring nutritional status, the mobility of N renders this approach less sensitive to differences in N status than whole plant analysis. Measurements of the N concentration of the entire standing biomass showed that the N concentration in the least productive sites in Jul was only 58% that of the most productive site. Whereas C to N ratio in standing biomass averaged 36.8 in optimal environments, this ratio averaged 62.8 in very severe environments. These observations strongly suggest that N limitation contributes to the poor growth observed in the least productive areas in this reconstructed marsh during periods of peak productivity.

Critical levels for tissue N in *S. alterniflora* have not been firmly established, complicating the use of tissue concentrations to assess N limitation in coastal marshes. Brandon (1973) reported that in Jun the N concentration of *S. alterniflora* growing along creek banks in a Louisiana marsh averaged 9.9 g N kg^{-1} whereas concentrations in shorter plants found inland averaged 7.9 g N kg^{-1}. Smart and Barko (1980) reported no increase in growth after tissue concentrations exceeded 15 g N kg^{-1} in

S. alterniflora grown in sand in a greenhouse, and suggested a critical tissue concentration of 7.3 g N kg^{-1}. Tyler et al. (2003) found that when very high rates of N fertilizer were applied (100 kg ha^{-1} $month^{-1}$) to stands of *S. alterniflora* in a Virginia coastal marsh tissue N concentrations in standing biomass increased slightly from 11-13 g N kg^{-1} to 14-15 g N kg^{-1}, though fertilization substantially increased biomass production.

Table 3-1 Seasonal means of N and C: N in uppermost leaves and aboveground biomass of *Spartina alterniflora* harvested from April 2004 to March, 2005 from environments with various levels of productivity. The areal accumulation (uptake) of N is also shown.

Category	Uppermost Leaves		Whole plant		
	N conc	C:N	N conc	C:N	Uptake
Apr-04	g N kg^{-1}	ratio	g N kg^{-1}	ratio	kg N ha^{-1}
Optimal	14.75	28.5	nd	nd	nd
Moderate	18.22	23.3	nd	nd	nd
Severe	14.59	28.2	nd	nd	nd
Very severe	14.81	28.6	nd	nd	nd
Jul-04					
Optimal	11.47	37.3	11.41a	36.8a	222
Moderate	11.58	37.1	8.93b	49.1b	123
Severe	11.01	39.2	9.67b	44.9ab	71
Very severe	9.63	43.3	6.69a	62.8c	16
Nov-04					
Optimal	10.94	32.1	7.79	46.1	65
Moderate	14.12	25.6	8.09	43.4	29
Severe	12.74	28.0	8.56	42	30
Very severe	11.05	31.8	6.76	51.9	14
Mar-05					
Optimal	10.69	36.0	12.69	31.3	59
Moderate	10.96	35.1	14.11	28.3	34
Severe	11.71	32.7	9.93	38.4	18
Very severe	13.45	28.4	11.47	33.3	17

In the study reported here, the relationship between productivity and N

concentrations in tissue were most evident in Jul when concentrations at sites showing optimal growth averaged 11.4 mg N kg^{-1} in both upper leaves and standing biomass. The ratio of C to N associated with optimal growth leaves and standing biomass were also similar in Jul and averaged 37:1. In contrast, upper leaf concentrations in less productive sites sampled in Jul exceeded standing biomass concentrations. This observation supports the conclusion that N assimilation in severely stressed sites was not adequate to compensate for the rate of C fixation, and translocation of N from older to younger tissue occurred.

During the cool months of winter, upper leaf N concentrations remained relatively constant whereas whole plant N concentrations tended to increase in all samples and differences between N concentration and productivity were no longer evident. Similar seasonal patterns in the N content in aboveground biomass have been reported by Gallagher et al. (1980) and Hopkinson and Schubauer (1984) for stands of *S. alterniflora* growing in natural marsh. Recruitment of small shoots is greatest during winter (Hopkinson et al. 1980), whereas productivity is highest in spring. Since the highest concentration of nitrogen was also observed during Apr, a large nutrient investment by the plant in production of new leaf material is indicated (Chapin and Slack 1979). The decline in nitrogen concentration in summer is probably due to the inability of soil reserves and net accumulation to keep pace with the enhanced rate of carbon fixation.

During Jul, sites with optimal productivity contained an average of 222 kg N ha^{-1}

in standing biomass, whereas the aerial portion of *S. alterniflora* in very severe environments contained only 16 kg N ha^{-1}. By Nov, N in standing biomass had declined 87% in the most productive sites and only 24% in the least productive sites. These declines underscore the potential of *S. alterniflora* to contribute crude protein to coastal ecosystems, and suggest that severely stressed plants do not play a significant role in N cycling in coastal marsh systems.

3.3.2 Sediment N and C

Table 3-2 Annual means of organic C, total N, and C: N in the surface 20 cm of sediment in sites with various levels of *S. alterniflora* productivity

	Organic C	Total N	C:N
	g C kg^{-1}	*g N kg^{-1}*	
Barren	6.47a	0.23a	32.1a
Very severe	7.36ab	0.32b	29.0a
Severe	9.18b	0.39bc	26.6ab
Moderate	11.18c	0.46c	26.7ab
Optimal	11.05c	0.44c	29.8a
Open water	15.24d	0.92d	22.55b

The sediments of more productive sites tended to contain more organic matter and more total N than less productive sites (Table 3-2) with the exception of open water areas adjacent to the vegetated shoreline where prolonged daily flooding limited colonization by *S. alterniflora*. Sites that had remained barren since deposition of dredge spoil contained the lowest amounts of organic C (6.47 g kg^{-1}), the lowest amounts of total N (0.23 g kg^{-1}), and the highest C: N ratio. These amounts of organic C and total N were about half those found at more productive sites, suggesting that the amounts of organic matter deposited in the surface sediment during wetland restoration is a primary factor

influencing later primary productivity. There was no detectable change in the amounts of organic C and total N found in samples collected between Apr 04 and Mar 05, but it is plausible that organic matter will continue to increase in the more productive sites where deposition was much greater than in less productive sites. The substantially lower levels of N and C returned as dead biomass in the less productive sites ensures that organic accumulation will remain low in these sites.

Table 3-3 Concentrations of ammonium and nitrate in sediment pore water collected between Apr 2004 to Mar 2005 at sites with various levels of productivity.

	Apr 04		Jul 04		Nov 04	
Category	NH_4^+	NO_3^-	NH_4^+	NO_3^-	NH_4^+	NO_3^-
	mg N L^{-1}					
Barren	0.067	0.034	0.217	0.199	0.085	0.030
Very severe	0.020	0.028	0.276	0.221	0.040	0.017
Severe	0.042	0.009	0.220	0.197	0.087	0.018
Moderate	0.052	0.007	0.289	0.274	0.036	0.016
Optimal	0.159	0.020	0.132	0.100	0.014	0.010
Open water	0.041	0.005	0.218	0.131	0.181	0.028

The levels of soluble inorganic N in sediments (Table 3-3) were greater in Jul than in the preceding Apr, and Nov. In 'optimal' environments, the amounts of NH_4^+ plus NO_3^- increased from 0.18 to 0.23 mg N L^{-1} during this period of vigorous vegetative growth. The greater accumulations of readily available N in sediments supporting lower levels of productivity during Jul indicates that factors other than N availability were influencing N uptake and primary production. In Jul, pore water contained approximately equal quantities of N as NH_4^+ and NO_3^-. In other seasons, NH_4^+ accounted for about 75% of soluble N in sediment pore water.

3.3.2 P Assimilation

Concentrations of P in upper leaves and standing biomass were not strongly related to productivity, suggesting that P availability was adequate to support the levels of growth observed at various sites. Table 3-4 shows that the P concentrations in the uppermost fully expanded leaves of volunteer *S. alterniflora* ranged from 0.94 to 4.79 g P kg^{-1}. Concentrations in standing biomass ranged from 0.84 g P kg^{-1} in severely stressed plants harvested in Jul to 3.09 g P kg^{-1} in plants displaying the highest level of growth in Mar. All of these values greatly exceed the critical value of 0.44 g P kg^{-1} proposed by Smart and Barko (1980) on the basis of a greenhouse study using *S. alterniflora* grown from seed. The values reported in Table 3-4, however, are within the range of tissue P concentrations reported by McHugh and Dighton (2004) using a simulated marsh system, whose data suggest a critical value for tissue P substantially greater than that suggested by Smart and Barko (1980). For comparison, critical levels of tissue P reported for rice range from 1.0 to 1.8 g P kg^{-1} and those for upland grasses range generally range from 2.0 to 3.5 g P kg^{-1} (Jones et al.1991).

Overall, tissue P levels were lowest in the Jul following a period of rapid growth, and were highest in Mar prior to spring growth. The two environments most likely to be limited by P availability were those displaying the lowest and highest levels of productivity in Jul. The ratio of C to P in upper leaves and standing biomass harvested from very severe environments in Jul exceeded 400:1, whereas only the C:P of standing biomass exceeded this ratio in sites classified as optimal.

Table 3-4 Seasonal means of P and C:P in uppermost leaves and standing biomass of *Spartina alterniflora* harvested between April 2004 to March 2005 from environments with various levels of productivity. The areal accumulation (uptake) of P is also shown

Category	Uppermost Leaves		Whole plant		
	P conc.	C:P	P conc.	C:P	Uptake
Apr-04	g P kg^{-1}	ratio	g P kg^{-1}	ratio	kg Pha^{-1}
Optimal	1.65	254.9	nd	nd	Nd
Moderate	1.78	238.5	nd	nd	Nd
Severe	1.98	207.7	nd	nd	Nd
Very severe	2.32	182.3	nd	nd	Nd
Jul-04					
Optimal	1.34	319.1	1.05	400.2	23.6
Moderate	1.48	289.8	1.25	350.4	17.5
Severe	1.59	270.2	1.17	371.4	8.7
Very severe	0.94	443.3	0.84	500.2	2.1
Nov-04					
Optimal	2.05	171.4	1.26	284.7	17.3
Moderate	1.94	186.7	1.29	272.3	5.2
Severe	1.92	185.8	1.24	290.1	4.2
Very severe	1.96	179.4	1.26	278.7	1.1
Mar-05					
Optimal	3.81	101.1	3.09	128.6	14.6
Moderate	3.45	111.5	3.02	132.2	4.8
Severe	3.39	112.8	2.91	131.1	3.8
Very severe	4.79	79.9	3.5	109.1	0.7

The amounts of P accumulated in standing biomass ranged from as little as 0.7 g ha^{-1} in severely stressed sites harvested in Mar to as much as 23.6 g ha^{-1} in highly productive sites harvested in Jul. Overall, about 59% of the P accumulated in Jul was conserved during the winter. Expressing the amounts of P accumulated in Mar as a percentage of amounts present in Jul indicate that the more productive sites retained 61% of their P whereas the less productive sites retained only 33%.

Analysis of the amounts of total P or 'available' P showed no significant

relationship to the overall productivity of volunteer stands, though the results were highly variable (Table 3-5). The inability of soil measurements to reflect differences in P uptake by *S. alterniflora* with various levels of productivity may have occurred because factors other than the availability of P in sediments strongly influence plant uptake. It is also possible that the sediment analyses failed to accurately express differences in availability. The method used to assess P availability (Bray's II) employs a strong acid that quite possibly over estimated the amounts of P available at the high pH levels in these soils.

Table 3-5 Mean annual pH and concentrations of total and 'available P' of sediments located in various areas of productivity.

	pH	Total P	Bray's P
		mg kg^{-1}	mg kg^{-1}
Barren	7.8	333.5	17.0
Very severe	7.8	291.3	15.7
Severe	7.8	352.0	16.3
Moderate	8.0	346.9	14.8
Optimal	8.0	275.8	17.0
Open water	7.9	372.1	14.7

3.4 CONCLUSIONS

Comparisons of tissue concentrations and uptake of N indicate that N deficiency is a primary determinant of overall productivity of *S. alterniflora* voluntarily colonizing marsh recently constructed from spoil obtained by hydraulic dredging of channel sediments in southern Louisiana. Tissues analyses indicate that concentrations >11 g N kg^{-1} in either uppermost leaves or standing biomass are sufficient for optimum

productivity. The most productive sites contained 222 kg N ha^{-1} in their standing biomass in summer, and shed 87% of these N during fall die back. The low productivity observed in very severely stressed environments greatly reduces their ability to contribute to N cycling in new marsh. While insufficient N uptake contributed to low productivity, other adverse factors clearly influenced growth in very severely stressed environments. Sites displaying higher levels of productivity generally contained greater amounts of organic C and total N, and contained nearly twice the organic C as sites that remained barren for 24 months after marsh construction. The organic C and total N contents sediments in optimal environments were 11 g C kg^{-1} and 0.44 g N kg^{-1}, respectively. Phosphorous uptake appeared to be adequate throughout the study, with the possible exceptions occasional limitations in summer. Tissue concentrations >1.4 g P kg^{-1} in uppermost leaves and 1.1-1.2 g P kg^{-1} in living standing biomass appear to be sufficient even during periods of rapid vegetative growth.

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